U.S. Department
of Commerce

Volume 95
Number 1
January 1997

Fishery Bulletin

U.S. Department of Commerce
Michael Kantor
Secretary

National Oceanic and Atmospheric Administration
D. James Baker
Under Secretary for Oceans and Atmosphere

National Marine Fisheries Service
Rolland A. Schmitten
Assistant Administrator for Fisheries

Fishery Bulletin

Scientific Editor
Dr. John B. Pearce

Editorial Assistant
Kimberly T. Murray
Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA
166 Water Street
Woods Hole, Massachusetts 02543-1097

Editorial Committee
Dr. Andrew E. Dizon National Marine Fisheries Service
Dr. Harlyn O. Halvorson University of Massachusetts, Dartmouth
Dr. Ronald W. Hardy National Marine Fisheries Service
Dr. Linda L. Jones National Marine Fisheries Service
Dr. Richard D. Methot National Marine Fisheries Service
Dr. Theodore W. Pietsch University of Washington
Dr. Joseph E. Powers National Marine Fisheries Service
Dr. Fredric M. Serchuk National Marine Fisheries Service
Dr. Tim D. Smith National Marine Fisheries Service

Managing Editor
Sharyn Matriotti
National Marine Fisheries Service
Scientific Publications Office
7600 Sand Point Way NE, BIN C15700
Seattle, Washington 98115-0070

The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Periodicals postage is paid at Seattle, Wash., and additional offices. POSTMASTER send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, Attn: Chief, Mail List Branch, Mail Stop SSOM, Washington, DC 20402-9373.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $32.00 domestic and $40.00 foreign. Cost per single issue: $13.00 domestic and $16.25 foreign. See back page for order form.

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

U.S. Department
of Commerce
Seattle, Washington

Volume 95
Number 1
January 1997

Fishery Bulletin

Contents

Articles

1 **Bertram, Douglas F., Thomas J. Miller, and William C. Leggett**
Individual variation in growth and development during the early life stages of winter flounder, *Pleuronectes americanus*

11 **Crockford, Susan J.**
Archeological evidence of large northern bluefin tuna, *Thunnus thynnus,* in coastal waters of British Columbia and northern Washington

25 **Fisher, Joseph P., and William G. Pearcy**
Dietary overlap of juvenile fall- and spring-run chinook salmon, *Oncorhynchus tshawytscha,* in Coos Bay, Oregon

39 **Goodyear, C. Phillip**
Fish age determined from length: an evaluation of three methods using simulated red snapper data

47 **Griffiths, Marc H.**
The life history and stock separation of silver kob, *Argyrosomus inodorus,* in South African waters

68 **Hampton, John**
Estimates of tag-reporting and tag-shedding rates in a large-scale tuna tagging experiment in the western tropical Pacific Ocean

80 **Hinton, Michael G., Ronald G. Taylor, and Michael D. Murphy**
Use of gonad indices to estimate the status of reproductive activity of female swordfish, *Xiphias gladius*: a validated classification method

85 **Kane, Joseph**
Persistent spatial and temporal abundance patterns for late-stage copepodites of *Centropages hamatus* (Copepoda: Calanoida) in the U.S. northeast continental shelf ecosystem

The National Marine Fisheries Service (NMFS) does not approve, recommend, or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends, or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

99 **Livingston, Mary E., Marianne Vignaux, and Kathy A. Schofield**
Estimating the annual proportion of nonspawning adults in New Zealand hoki, *Macruronus novaezelandiae*

114 **McKenna, James E., Jr.**
Structure and dynamics of the fishery harvest in Broward County, Florida, during 1989

126 **McQuinn, Ian H.**
Year-class twinning in sympatric seasonal spawning populations of Atlantic herring, *Clupea harengus*

137 **Parrish, Frank A., Edward E. DeMartini, and Denise M. Ellis**
Nursery habitat in relation to production of juvenile pink snapper, *Pristipomoides filamentosus,* in the Hawaiian Archipelago

149 **Restrepo, Victor R., and Joseph E. Powers**
Application of high-breakdown robust regression to tuned stock assessment models

161 **Shi, Yunbing, Donald R. Gunderson, and Patrick J. Sullivan**
Growth and survival of 0^+ English sole, *Pleuronectes vetulus,* in estuaries and adjacent nearshore waters off Washington

Notes

174 **Richardson, Linda R., and John R. Gold**
Mitochondrial DNA diversity in and population structure of red grouper, *Epinephelus morio,* from the Gulf of Mexico

180 **Zavala-González, Alfredo, and Eric Mellink**
Entanglement of California sea lions, *Zalophus californianus californianus,* in fishing gear in the central-northern part of the Gulf of California, Mexico

185 *Erratum*

186 *Subscription form*

Individual variation in growth and development during the early life stages of winter flounder, *Pleuronectes americanus*

Douglas F. Bertram*
Thomas J. Miller**
William C. Leggett***
Department of Biology, McGill University
1205 Avenue Docteur Penfield,
Montreal, QC, Canada H3A 1B1

Abstract.—We studied phenotypic variation in larval and juvenile growth and development, using laboratory-reared winter flounder, *Pleuronectes americanus*. Larvae were reared individually to metamorphosis and beyond and were measured at weekly intervals. Growth in length was rapid until 30 d but slowed thereafter until metamorphosis. Standard length peaked and often declined as metamorphosis approached, and notochord length decreased during flexion. Length at 30 d (an index of larval growth rate) was inversely related to age at metamorphosis, confirming previous assertions that larvae that grow rapidly also develop most rapidly. The relation between growth rate and larval-period duration, however, was not straightforward. The time from the day of peak larval length until metamorphosis (7–35 d) appeared to be inversely related to larval growth rate. Juvenile growth rates during the first 3 weeks following metamorphosis were unrelated to length at 30 d. Additional juveniles, reared in groups as larvae and tracked as individuals following metamorphosis, showed no change in growth rates during the first 4 weeks of the juvenile period in relation to increasing age at metamorphosis or larval growth rates. These results are consistent with earlier findings that size at age does not diverge continually throughout the larval and juvenile periods. Compensatory juvenile growth among fish that grew slowly as larvae was observed but not to the same extent as previously reported. We emphasize the utility of the individual-based approach for identifying patterns of phenotypic variability in growth and development during the early life stages in fishes.

Manuscript accepted 13 August 1996.
Fishery Bulletin 95:1–10 (1997).

Mechanisms controlling survival and recruitment of fishes operate at the level of the individual (Crowder et al., 1992). Further, small initial differences among individual larvae and juveniles within fish populations may have disproportionate effects on the probability of their survival (Crowder et al., 1992; Rice et al., 1993). Consequently, research programs in fisheries have begun to focus on phenotypic variability within cohorts in an effort to identify particular traits that may be unique to the small minority of survivors (Fritz et al., 1990; Taggart and Frank, 1990). If survivors are not random subsets of the original cohort, interpretations of recruitment processes based upon analyses of population averages are likely to be misleading (Pepin and Miller, 1993). Consequently, individual-based approaches are increasingly favored (Crowder et al., 1992). However, there have been few quantitative measurements of either individual variation in early life history traits of fishes or in their survival consequences (but see Rosenberg and Haugen, 1982; Rice et al., 1987; Chambers et al., 1989; Chambers and Leggett, 1992; D'Amours, 1992; Bertram and Leggett, 1994; Lochmann et al., 1995; Miller et al., 1995). In theory, longitudinal data can be obtained from sequential measurements of individuals or from back calculations of size at age from otolith microstructure.

Variation in larval growth rates is widely believed to be a central feature in year-class formation in fishes (Leggett and Deblois, 1994). Traditionally, growth parameters are estimated from a restricted number of samples of the population. Each sample includes a range of fish lengths and ages. Importantly, each fish provides only a single estimate of length at age. Such data are termed cross-sectioned. The calculated growth parameters represent composite pictures and cannot reveal variability among the growth patterns of individuals simply because they aggregate data at a level higher than the individual. Chambers and Miller (1995) have discussed the effects of the level of aggregation of data on the inferences that can be made. In addition, composite growth curves

* Present address: Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada 156 V5A. E-mail address: dbertram@sfu.ca
** Present address: The University of Maryland System, Chesapeake Biological Laboratory, P.O. Box 38, Solomons, Maryland 20688-0038.
*** Present address: Queen's University, 206 Richardson Hall, Kingston, Ontario, Canada K7L 3N6.

are subject to several potential biases (Chambers and Miller, 1995). For example, composite curves are not accurate in cases where mortality of individual age classes are biased towards small or large individuals (Litvak and Leggett, 1992; Pepin et al., 1992). Hence, if the survival consequences of variability in growth rates are to be evaluated adequately, individual phenotypic variability in growth must be quantified (Lynch and Arnold, 1988; Chambers, 1993). This requires that longitudinal data based upon repeated measures of individuals be collected. These problems are illustrated in the following example. Consider a cohort of 220 larvae with an average size of 5.5 mm and a uniform size distribution of 20 larvae in each of ten 0.1-mm size classes from 5 to 6 mm. In a hypothetical 7-d interval, no larval growth occurs, but a gape-limited predator consumes all larvae less than 5.5 mm, leaving 120 larvae with an average size of 5.75 mm. If only cross-sectional data were available, the larval growth rate was estimated as 0.11 mm/d for the 7-d interval. However, if longitudinal data were available (i.e. measurements of survivors at the beginning and end of the week), it would be clear that no growth had occurred.

Bertram et al. (1993) have argued that the dynamics of larval and juvenile growth rates should be examined in unison, rather than separately. Using laboratory-reared winter flounder, *Pleuronectes americanus*, they have shown that size-at-age trajectories do not diverge continually during the larval and juvenile periods. In fact, juvenile size-at-age trajectories converge because fish that grew slowly as larvae compensated for their slow growth by growing rapidly as juveniles. However, Bertram et al. (1993) assumed that larval growth was linear; therefore juvenile fish used in their experiments were pooled into groups. This approach precluded the study of individual phenotypic variability. The objectives of the present study were 1) to provide estimates of the individual variability in growth rate in fish during early life stages because it is upon this individual variability that phenotypic selection acts and 2) to evaluate the validity of previous estimates of larval growth rate. Also, we explore how individual variation in larval growth affects growth during the subsequent juvenile period.

Methods

Rearing protocol

The research in this study was conducted at the Huntsman Marine Science Centre, St. Andrews, New Brunswick, during summer 1991. In May, adult winter flounder were collected from Passamaquoddy Bay with a bottom trawl and held at ambient seawater temperature (7–8°C). When ripe, eggs from individual females were combined with sperm pooled from three males to create half-sibling families. Families were maintained separately throughout the study. Fertilized eggs were placed in a slurry of diatomateous earth for 12 h following fertilization to prevent clumping. Incubation temperature was 7 (±0.5)°C (mean ± SD). At approximately 24-h after fertilization, the eggs were immersed in solutions of penicillin (0.0158 g/L) and streptomycin (0.02 g/L) for 24 h. Filtered, UV-sterilized seawater was replaced every 2–3 d until hatching commenced at approximately 14 d after fertilization.

Upon hatching, 118 larvae from two families (families 1 and 2) were individually stocked into black cylindrical 0.4-L containers (15 cm diameter × 6.5 cm high) with clear plexiglass bottoms. Water temperature was maintained at 10 (±0.5)°C in a temperature controlled room with a 16:8 day:night photoperiod. At weekly intervals, 75% of the water was removed from each container and replaced with UV-sterilized filtered seawater. Additional "reserve" larvae from the same families were reared in groups under identical conditions in 18-L cylindrical, black plastic containers. Individual larvae that died within the first 3 weeks were replaced with siblings from the appropriate reserve group.

Larvae were also reared in groups in 38-L aquaria covered externally with black plastic. Five aquaria were each stocked with four-hundred 1-d-old larvae drawn from another half-sibling family (family 3). Temperatures in the aquaria were maintained at 10 (±0.5)°C. At weekly intervals, 3 liters of water were removed from each aquarium and replaced with UV-sterilized filtered seawater. Dead larvae were siphoned regularly from the tank.

All larvae were fed *Brachionus* sp. at 2 /(mL·d) until the end of week 7. Rotifers were cultured by using *Isochrysis* sp. and *Chaetoceros* sp. Twenty-four hours prior to being fed to larvae, rotifers were provided with Microfeast artificial plankton (Provesta Corporation) to enhance their nutritional quality. From the end of week 5 onwards, larvae were also offered *Artemia* nauplii (0.25/[mL·d]). Nauplii were enriched with Microfeast 24 h prior to use.

At metamorphosis, larvae from family 3, which had been reared in groups, were individually stocked into 0.4-L rearing containers (see above) to examine juvenile growth. To standardize the developmental stage of individuals used in this study, we used only fish whose left eye had just crossed the midline on its migration to the right side of the body (stage H of Seikai et al., 1986). All fish that metamorphosed on

the same day were treated as a discrete cohort. The creation of these cohorts was repeated at intervals of 3–8 d until all fish had metamorphosed. Table 1 summarizes the rearing conditions for the 3 families used in the study.

Table 1
Summary of rearing conditions and filming schedules for the 3 families used in the study.

	Family 1	Family 2	Family 3
Larval container size (L)	0.4	0.4	38
Number of larvae/container	1	1	400
Weekly measures of larvae	Yes	Yes	No
Juvenile container size (L)	0.4	0.4	0.4
Number of juveniles/container	1	1	1
Weekly measures of juveniles	Yes	Yes	Yes

At weekly intervals, length data on individual larvae were recorded by using a dissecting microscope linked to a video system at 6× magnification. Larvae were filmed without being removed from their rearing containers. Fish were not anesthetized at any time. Larval movement was restricted by confining larvae within a 6-cm diameter plexiglass ring placed within the rearing container. Length data were collected only when fish were in the horizontal plane. To account for variation in the position of the larvae in the vertical plane, we constructed a small set of "stairs" with a plastic ruler segment attached at each level. After filming each larva, we immediately calibrated the image against the ruler segment that was in focus. For fish that were close to, or past, metamorphosis, the process of filming was simplified because these fish generally remained motionless on the bottom of the container. Following metamorphosis, individual juveniles were filmed weekly for up to 4 weeks, when rearing was terminated. Standard lengths of all fish were obtained by using an image analysis system (Optimus vers. 3.11, Bioscan Corporation, Seattle, WA). We used the image analysis system to "capture" two images for each fish for estimating standard length at age and used the largest value in all analyses.

Analysis

We constructed individual growth trajectories for larvae that survived until metamorphosis, using spline functions fitted to repeated measures of size at age. Individual larval growth trajectories were based on between 3 and 9 weekly observations per larva. Individual growth trajectories were examined quantitatively by using four indexes: 1) larval size at 30 ±1 d (roughly midway through the development period, an index of larval growth rate [e.g. Travis, 1981]); 2) average larval growth rates, defined as the difference between the length at metamorphosis and the mean length at hatching for the family divided by the time elapsed between the two events; 3) latency period, defined as the time between the age at which maximum larval length was attained and the time of metamorphosis; and 4) larval-period duration, defined as the age at metamorphosis. Correlation analyses (Pearson's correlation coefficient) were used to examine the relationships among pairs of the above variables for individual larvae. Variables were tested for normality with normal probability plots (Wilkinson, 1990). When heteroscedasticity was detected with techniques outlined in Zar (1984), variables were log-transformed. For comparison with the individual growth trajectories, we also constructed a composite size-at-age plot by using data for all larvae used in the study.

We checked for size-dependent mortality during the first part of the larval period by comparing the length of those fish that lived until their next weekly measurement with those that died during that time, using t-tests for independent samples. Size-dependent analyses were conducted for larvae after hatching (1–2 d); week 1 (8–9 d); week 2 (15–16 d); and week 3 (22–23 d). Group-reared larvae that were used as replacements for fish that died during the first 3 weeks were not included in the analysis.

Individual juvenile growth rates were estimated from the slope of a least squares fitted to weekly measures of individual size at age from metamorphosis to week 3 of the juvenile period. Thus, growth estimates were based upon up to 4 size-at-age measurements. Growth parameters were not calculated when less than 3 size-at-age measurements were available. We examined the correlations between juvenile growth rates and both age at metamorphosis and length at 30 d. Juvenile growth rates were also examined in relation to Bertram et al.'s (1993) measure of average larval growth rate estimated as the difference between the mean length at metamorphosis for fish that metamorphosed on the same day and the mean size at hatching for the family, divided by the number of days between the 2 events.

For comparison with the work of Bertram et al. (1993), we restricted the analysis of juvenile growth to weeks 1 through 4 for fish that had been reared together as larvae. The relation between juvenile growth rates and age at metamorphosis was examined by using regression and correlation analyses. Similar analyses were performed to examine the re-

lationship between juvenile growth rates and average larval growth rate. For fish that had metamorphosed early, measurements of size at age were available until week 7 of the juvenile period. For these individuals we compared growth rates during weeks 1–4 with those during weeks 5–7, using a paired t-test.

Results

Individually reared larvae

Thirty-two individually reared fish, 31 of which were from a single family (family 1), survived until metamorphosis. For 5 of these fish, weekly measures were available from hatching to metamorphosis. For the remaining 27 larvae weekly measures began at day 22. We could not detect size-dependent mortality in the weeks following: hatching (t=1.83, df=116), week 1 (t=0.18, df=87), week 2 (t=1.4, df=32), or week 3 (t=0.21, df=11). Data from the 32 fish provided estimates of individual larval growth trajectories (Fig. 1A). The trajectories exhibited considerable phenotypic variation in size at age, maximum larval size, size at metamorphosis, latency period, and the duration of the larval period (Fig. 1A). To demonstrate the loss of information introduced by basing growth parameters on cross-sectional data, we treated the original individual-level longitudinal data as cross-sectional. When individual larval sizes were depicted in this composite fashion (Fig. 1B), mean larval length at age increased rapidly from day 1 until day 30 and then leveled off. Important information, however, can be obtained only from cross-sectional data. For example, coefficients of variation (CV) for length at age increased from 0.07 on day 1 to 0.12 on day 30 but declined subsequently and leveled off at approximately 0.08.

The largest larvae at 30 d were also largest at 22 d (r=0.66, n=18, P=0.03) and at 36 d (r=0.5, n=18, P=0.034), indicating positive covariance in size at age for individually reared larvae that were alive at each of those ages. There was a significant positive relationship between larval length at 30 d and maximum larval size (r=0.6, n=27, P=0.001). However, larval length at 30 d and age at metamorphosis were negatively correlated (n=27, r=–0.589, P=0.001; Fig. 2A). The negative correlation coefficient between size at 30 d and age at metamorphosis was larger than correlation coefficients calculated for all other age classes. Average larval growth rate and length at 30 d were positively correlated (n=25, r=0.49, P=0.01; Fig. 2B).

The age of maximum larval size (log-transformed) was negatively correlated to length at 30 d (r=–0.71, n=27, P<0.001; Fig. 3A). The latency period (range:7–35 d; 14.4 ±7.5 d, n=31)(log-transformed) was inversely related to age of maximum larval size (r=–0.58, n=31, P=0.001; Fig. 3B). In contrast, the latency period showed a positive trend with increasing length at 30 d, but the relationship was not significant (r=0.2, n=26, P=0.38). Age at metamorphosis ranged from 44 d to 71 d (55.2±7.9 d). Length at metamorphosis ranged from 6.1 mm to 7.5 mm (6.6 ±0.3 mm). Length and age at metamorphosis were positively correlated for individually reared larvae (r=0.46, n=29, P=0.012).

Among individually reared larvae, subsequent juvenile growth rate during the first 3 weeks of the juvenile stage bore no relation to age at metamor-

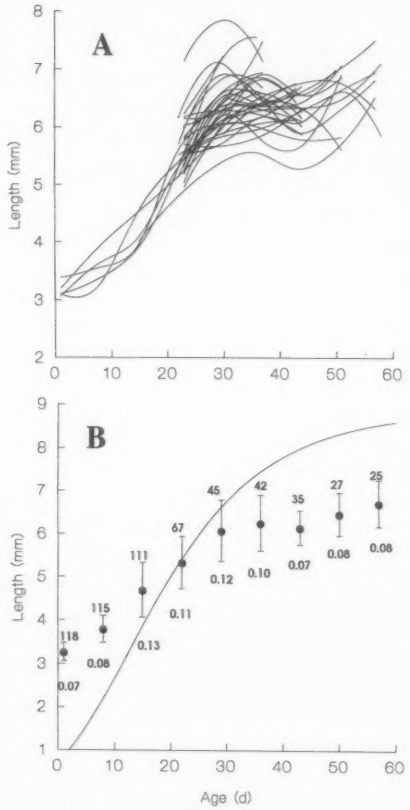


Figure 1

(**A**) Growth trajectories for individual laboratory-reared winter flounder, *Pleuronectes americanus*, larvae (n=32) based upon spline functions fitted to repeated weekly measures of standard length. Larval standard length (mean ±SD) versus age. (**B**) The sample size and CV for each age class are given above and below the error bar (respectively). Also shown is the Gompertz curve based upon the equation reported by Jearld et al. (1993) for winter flounder.

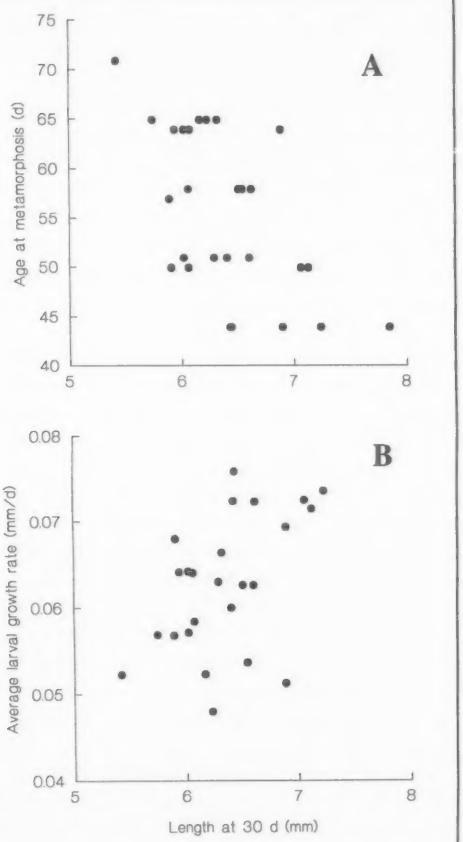


Figure 2

(A) Age at metamorphosis versus length at 30 d. **(B)** The relationship between average larval growth rate and length at 30 d.

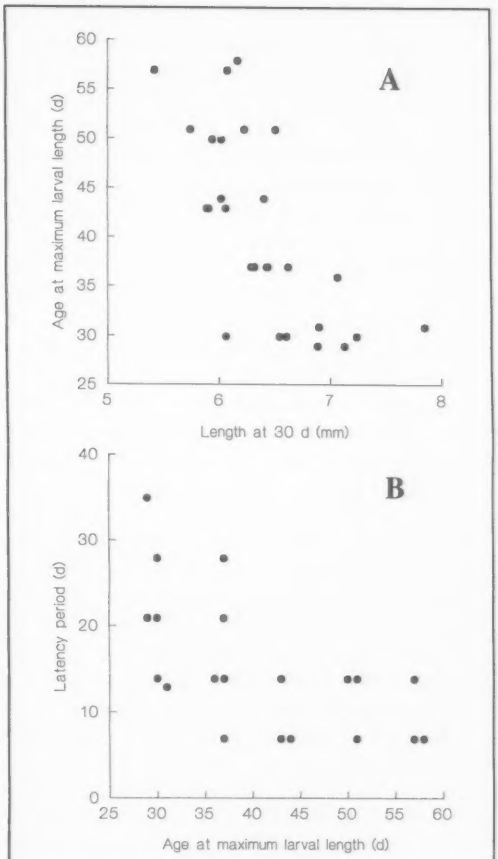


Figure 3

(A) Age at maximum larval length (untransformed) versus length at 30 d. **(B)** Latency period (untransformed) versus the age at maximum larval length.

phosis (r=0.22, n=11, P=0.52; Fig. 4A). Similarly, juvenile growth rate showed no relationship to length at 30 d (r=–0.001, n=10, P=0.99, Fig. 4B). For comparative purposes, juvenile growth rate was also regressed against the measure of larval growth rate used by Bertram et al. (1993). The slope of the relationship, –0.18 mm/d, although not significantly different from 0, was identical to that reported by Bertram et al. (1993).

Group-reared larvae

Length at metamorphosis was independent of age at metamorphosis among members of family 3 (r=–0.09, n=205, P=0.23) reared in groups as larvae and individually as juveniles. (Note that 175 of these larvae came from a single rearing aquarium and that the remainder were also from a single tank.) Length at metamorphosis ranged from 5.6 mm to 7.36 mm (6.6 ±0.3 mm). Age at metamorphosis ranged from 32 d to 59 d (42.6 [(±6.7] d). Individual growth rates during weeks 1–4 of the juvenile period were unrelated to age at metamorphosis (r=0.055, n=52, P=0.71; Fig. 5A). Juvenile growth rates were unrelated to larval growth rates (r=0.14, n=52, P=0.322; Fig 5B). Because juvenile growth rates were equivalent, we pooled cohorts that metamorphosed at different times on the basis of the number of days after metamorphosis. Coefficients of variation for size-at-d postmetamorphosis were unrelated to postmetamorphic age (weeks 1–4) and never exceeded 0.08.

Individual juveniles exhibited significantly faster growth rates during weeks 1–4 than during weeks 5–7 (t=9.45, df=17, P<0.0001).

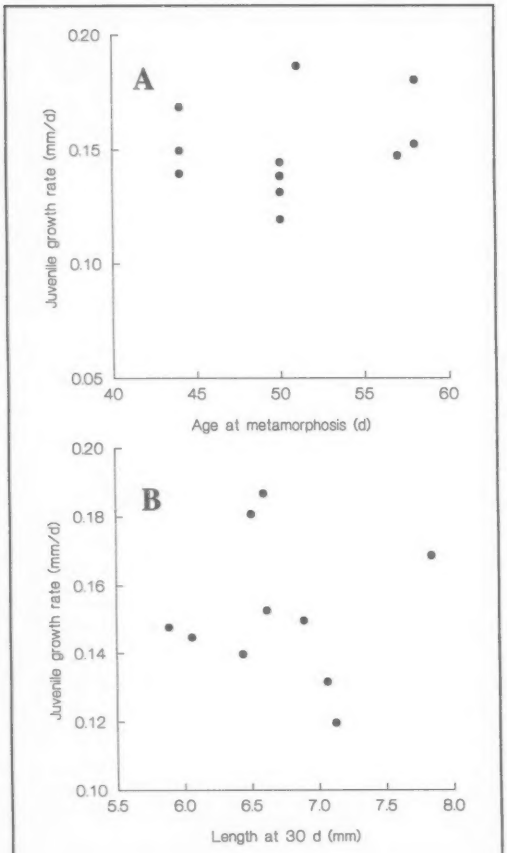


Figure 4

Larval and juvenile growth for fish reared individually in both periods. (**A**) Growth rate from week 0 to week 3 of the juvenile period versus age at metamorphosis. (**B**) Growth rate from week 0 to week 3 of the juvenile period versus length at 30 d, an index of larval growth rate.

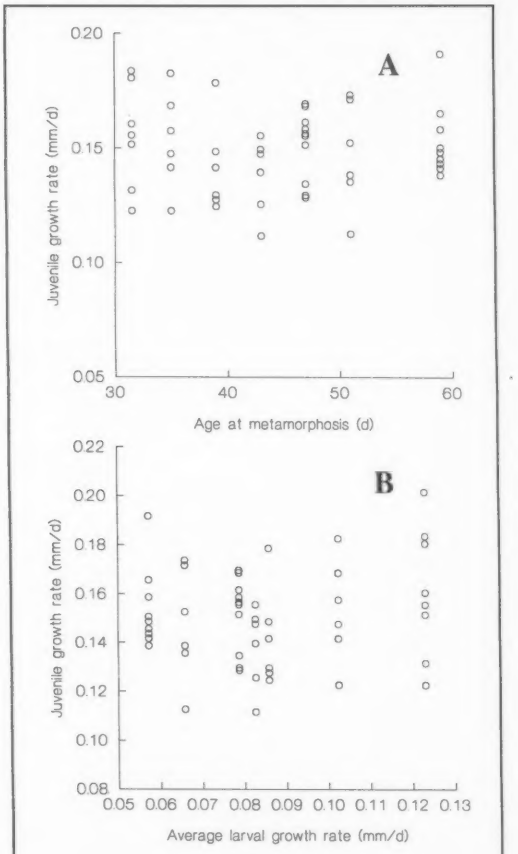


Figure 5

Larval and juvenile growth for fish reared individually (n=52) as juveniles. (**A**) Growth rate during weeks 1–4 of the juvenile period versus age at metamorphosis. (**B**) Growth rate during weeks 1–4 of the juvenile period versus average larval growth rate.

Discussion

Our data on growth dynamics of larval fishes show that size at age is highly variable during the larval period. Patterns in CV's for size at age demonstrate that most of the variation upon which selection can act is found during the early to mid phase of the larval period. Chambers et al. (1988), who analyzed average growth rates of larvae reared in groups, also found that CV's for size at age increased from hatching to a peak of 0.135 at 28 d and subsequently declined as metamorphosis approached. In this study, most larval growth occurred during the first 30 d. Individual larvae that grew most rapidly and reached the largest size at about day 30, midway through the larval period, metamorphosed at the youngest ages. Travis (1981), who reared anuran larvae individually, also reported that age at metamorphosis was inversely related to size midway through the larval period. Despite the nonlinear growth observed, the length at 30 d and the average larval growth rate were positively correlated. Thus, the general conclusion (derived from those studies where average larval growth was used and larval growth was assumed to be linear) that rapid growth reduces the duration of the larval period is supported (Chambers and Leggett, 1987; Chambers et al., 1988; Bertram et al., 1993).

The relationship between larval growth rate and larval-period duration, however, may not be straightforward. Although larval growth rate is the primary factor influencing larval-period duration, its effects appear to be modified by the duration of the latency period. Larvae that grow rapidly tend to reach maximum larval length at an early age. However, individuals that reach maximum larval length at an early age have a longer latency period than those larvae that reach maximum length late in the larval period. This finding suggests that rapid growth is associated with a long latency period. Slower-growing larvae, in comparison, may reach metamorphosis at a later age but have a considerably shorter latency period. Moreover, this suggests that metamorphosis may require a minimum duration, independent of size. These findings are consistent with Ricklefs' (1973, 1979) hypothesized tradeoff between growth rate and the acquisition of mature tissue function in birds. In this connection, it is noteworthy that a tradeoff between growth rate and the rate of protein turnover has been documented for the mussel *Mytilus edulis* (Hawkins et al., 1986). Our findings are also consistent with Balon's (1990) suggestion that through epigenetic interactions, individuals within a clutch may form distinct developmental groups—some being more altricial and others more precocial.

Growth rate estimates will be biased if mortality is size dependent. Biased growth-rate estimates will, in turn, reduce estimates of variation in growth rate. However, the extent of variability in larval growth rates reported here are not due to size-dependent mortality. Our analysis could not detect size-dependent mortality, and there was no reduced variability in growth until the end of week 4. Survival to metamorphosis was relatively high (26 out of 53 [49%] from family 1) for individuals replaced on day 22. High survival from day 1 to metamorphosis (175 out of 400 [44%]) was also observed for group-reared larvae in one of the rearing aquaria for family 3. Importantly, the CV for size and age at metamorphosis was similar for the individual and group-reared larvae. The CV for age at metamorphosis was 0.14 and 0.17 for individually reared and group reared larvae (n =175), respectively. The CV for size at metamorphosis was 0.045 and 0.046 for individually reared and group-reared larvae (n=175), respectively. (Note that the CV's for age and size at metamorphosis for the full data set of group reared larvae [n=205] were indistinguishable from those reported above for the reduced data set [n=175]). The similarity of CV's for age and size at metamorphosis implies similar scope for variation in growth rate despite differences in the rearing protocol.

We used a small number of female broodstock. This small number of fish, however, did not preclude insight into the potential for variation in larval growth and development at the population and species level. Previous research on early life history traits in winter flounder has shown that most of the total variation in metamorphic traits (age and size at metamorphosis) occurred within rather than among maternal families (Chambers and Leggett, 1992). Differences between families in the relationship between size and age at metamorphosis (Chambers and Leggett, 1987; see below) and length at metamorphosis (Chambers and Leggett, 1992, Bertram et al., 1993), although detectable, appear small in comparison with the similarities between families for variation in age at metamorphosis. Indeed, Chambers and Leggett (1992) reported that most variation in age at metamorphosis resided within each rearing aquarium. The CV's for age and size at metamorphosis reported here are similar to those reported by Chambers and Leggett (1987) despite differences in rearing temperatures and origins of broodstock employed in the two studies. Chambers and Leggett (1992) developed several qualitative expectations for parental influences on larval flatfishes. They suggested that parentage is likely to influence larval traits but that its contribution to the total phenotypic variation in larvae is expected to diminish during the larval period. In addition, the degree of parental influence is likely to be trait-specific. The absence of parental effects on important traits such as larval-period duration (age at metamorphosis) supports the potential generality of our results on early life history traits based on few parents. Moreover, in the absence of field data, laboratory-based research such as this represents the only basis for characterizing and predicting the dynamics of patterns of individual larval growth and development.

The survival consequences of individual variation in larval growth and development reported here are presently unknown. We do not know whether individuals that grow rapidly and metamorphose at an early age have a survival advantage over those that grow more slowly and metamorphose at an older age. Despite the limited supporting evidence, there has been widespread acceptance of the hypothesis that rapid larval growth conveys a survival advantage because those individuals are large at age and often have a reduced larval-period duration (Bertram, 1993; Leggett and Deblois, 1994). D'Amours (1992) tested directly the hypothesis that rapid larval growth increases survival by using wild 0-group (17–47 d) Atlantic mackerel, *Scomber scombrus*. Comparing the otolith microstructure of larvae from one cohort captured at two different intervals in time, he found no evidence of higher survivorship among faster-growing larvae. In addition, two studies have

found that larvae that are small at age may, under certain circumstances, be less vulnerable to predation than are large members of a cohort (Litvak and Leggett, 1992; Pepin et al., 1992; Bertram, 1996). In flatfishes and in other fishes that switch habitats at metamorphosis, the time of transition is likely to be associated with high mortality. In recent laboratory experiments, Whiting and Able (1995) demonstrated that mortality from shrimp (*Crangon septemspinosa*) predation on settled winter flounder (10.1–14.5 mm) was twice that of presettled individuals (≤11 mm). Bertram and Leggett (1994), however, could detect no difference in shrimp-induced mortality for winter flounder that differed in either length or age at metamorphosis. In the present study, there was a positive relation between length and age at metamorphosis for individually reared winter flounder, but this trend was not evident from the larger sample of group-reared fish (see also Bertram et al., 1993). However, the results may not be strictly comparable because different families were used for the individual and group rearing. Chambers and Leggett (1987) reported a positive relation between length and age at metamorphosis for 8 of 18 families of laboratory-reared winter flounder from Newfoundland. The appropriate experiments have not been conducted to determine whether both large size and old age at metamorphosis reduce mortality due to predation. Therefore, to date, there is no firm basis for interpreting the survival consequences of the individual variation in larval growth and development patterns reported here.

The results of this study are consistent with Bertram et al.'s (1993) finding that size at age does not diverge continuously during the larval and juvenile periods. Overall, the results show that juvenile growth rates are parallel, despite differences in larval growth rates and age at metamorphosis. The parallel nature of juvenile growth rates shows that slow-growing larvae partially compensated for their small size at age by increasing their juvenile growth rates to a greater degree than did fish that grew rapidly as larvae. However, the compensatory growth among slow-growing larvae was not sufficient to cause convergence in juvenile size at age. If these growth rates are maintained, differences in size at age of juveniles that metamorphosed early and late would remain.

Previous work has shown that growth rates of group-reared fish were maintained from weeks 1–7 of the juvenile period (Bertram et al., 1993). In the present study, however, the growth rate of individually reared juveniles was slower in weeks 5–7 than during weeks 1–4. There is reason to believe that food availability was a factor in this difference. Juveniles reared in groups in 7-L containers were exposed to concentrations of 292 prey/d per fish. Juveniles reared individually in 0.4-L containers received 100 prey/d because rations were 0.25 *Artemia* nauplii/(mL·d) for both container sizes. Consequently, food availability may have limited the growth rate of individually-reared juveniles during weeks 5–7 when fish were relatively large and food requirements were maximal.

An important conclusion from this study is that the insight into the dynamics of larval growth and development was gained only because the data were presented as individual-based observations. Although the CV's of size at age would have been available if the weekly length measures of individuals had been pooled, the underlying growth dynamics and individual variability would have been concealed. Moreover, a single "growth" curve fit to such size-at-age data would not accurately reflect the growth patterns of individual larvae. In this connection, we point out that a recent description of winter flounder larval "growth," based upon reconstructions of size at age from otolith microstructure (Jearld et al., 1993), bears little resemblance to the individual growth trajectories shown here.

Darwin (1859) wrote: "No one supposes that all individuals of the same species are cast in the very same mould"; but it is only recently that fishery scientists have begun to investigate the potential population consequences of phenotypic variability in early life history stages. Because mechanisms controlling survival and recruitment of fishes operate at the level of the individual (Crowder et al., 1992), baseline estimates on phenotypic variability are required. This study clearly shows that rearing marine fish larvae individually in the laboratory can provide such estimates. We have shown that there is considerable variability in the dynamics of individual larval growth and development. Studies that examine the survival consequences of such variability represent a logical next step in research programs designed to provide a mechanistic understanding of the factors that affect survival during fish early life history.

Acknowledgments

We thank M. Litvak, F. Purton, and the staff of the Huntsman Marine Science Centre (HMSC) for their cooperation in this research. J. Farrell, S. Gutterman, and S. Whelan provided technical assistance. Financial support was provided by Natural Sciences and Engineering Research Council (NSERC) of Canada operating and strategic grants to WCL. Additional financial support to DFB was provided by a NSERC

post graduate scholarship, the Anne Vallée Ecological Fund Scholarship, and a HMSC graduate fellowship.

Literature cited

Balon, E. K.
1990. Epigenesis of an epigeneticist: the development of some alternative concepts on the early ontogeny and evolution of fishes. Guelph Ichthyol. Rev. 1:1–48.

Bertram, D. F.
1993. Growth, development and mortality in metazoan early life histories with particular reference to marine flatfish. Ph.D. thesis, McGill Univ., Montreal, 219 p.
1996. Size-dependent predation risk in larval fishes: mechanistic inferences and levels of analysis. Fish. Bull. 94: 371–373.

Bertram, D. F., R. C. Chambers, and W. C. Leggett.
1993. Negative correlations between larval and juvenile growth rates in winter flounder: the implications of compensatory growth for variation in size-at-age. Mar. Ecol. Prog. Ser. 96:209–215.

Bertram, D. F., and W. C. Leggett.
1994. Predation risk during the early life history periods of fishes: separating the effects of size and age. Mar. Ecol. Prog. Ser. 109:105–114.

Chambers, R. C.
1993. Phenotypic variability in fish populations and it representation in individual-based models. Trans. Am. Fish. Soc. 122:404–414.

Chambers, R. C., and W. C. Leggett.
1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. Can. J. Fish. Aquat. Sci. 44:1936–1947.
1992. Possible causes and consequences of variation in age and size at metamorphosis in flatfishes (Pleuronectiformes): an analysis at the individual, population and species levels. Netherlands J. Sea Res. 29:7–24.

Chambers, R. C., W. C. Leggett, and J. A. Brown.
1988. Variation in and among early life history traits of laboratory-reared winter flounder *Pseudopleuronectes americanus*. Mar. Ecol. Prog. Ser. 47:1–15.
1989. Egg size, female effects and the correlations between early life history traits of capelin, *Mallotus villosus*: an appraisal at the individual level. Fish. Bull. 87:515–523.

Chambers, R. C., and T. J. Miller.
1995. Evaluating fish growth by means of otolith increment analysis: special properties of individual level longitudinal data. *In* S. Campana, D. H. Secor, and J. M. Dean (eds.), Fish otolith research and application; proceedings of the international symposium, p. 155–175. Univ. South Carolina Press, Columbia, SC.

Crowder, L. B., J. A. Rice, T. J. Miller, and E. A. Marschall.
1992. Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes. *In* D. L. DeAngelis and L. J. Gross (eds.), Individual-based models and approaches in ecology: populations, communities, and ecosystems, p. 237–255. Chapman and Hall, New York, NY.

D'Amours, D.
1992. A test of the adaptive value of growth for juvenile (O-group) Atlantic mackerel (*Scomber scombrus*). *In* Y. de Lafontaine, T. T. Lambert, G. R. Lilly, W. D. McKone, and R. J. Miller (eds.), Juvenile stages: the missing link in fisheries research: report of a workshop, p. 127–131. Can. Tech. Rep. Fish. Aquat. Sci. 1890.

Darwin, C.
1859. The origin of species. (1968 ed.). Penguin, Harmondsworth, London.

Fritz, E. S., L. B. Crowder, and R. C. Francis.
1990. The National Oceanic and Atmospheric Administration plan for recruitment fisheries oceanography research. Fisheries 15:25–31.

Hawkins, A. J. S., B. L. Bayne, and A. J. Day.
1986. Protein turnover, physiological energetics and heterozygosity in the blue mussel, *Mytilus edulis*: the basis of variable age-specific growth. Proc. R. Soc. Lond. B. Biol. Sci. 229:161–176.

Jearld, A., Jr., S. L. Sass, and M. F. Davis.
1993. Early growth, behaviour and otolith development of the winter flounder, *Pleuronectes americanus*. Fish. Bull. 91:65–75.

Leggett, W. C., and E. Deblois.
1994. Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? Neth. J. Sea Res. 32:119–134.

Litvak, M. K., and W. C. Leggett.
1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Mar. Ecol. Prog. Ser. 81:13–24.

Lochmann, S. E., G. L. Maillet, K. T. Frank, and C. T. Taggart.
1995. Lipid class composition as a measure of nutritional condition in individual larval Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 52:1294–1306.

Lynch, M., and S. J. Arnold.
1988. The measurement of selection on size and growth. *In* B. Ebenman and L. Persson (eds.), Size-structured populations, p. 47–59. Springer Verlag, Berlin.

Miller, T. J., T. Herra, and W. C. Leggett.
1995. An individual-based analysis of the variability of eggs and their newly hatched larvae of Atlantic cod (*Gadus morhua*) on the Scotian Shelf. Can. J. Fish. Aquat. Sci. 52:1083–1093.

Pepin, P., and T. J. Miller.
1993. Potential use and abuse of general empirical models of early life history processes in fish. Can. J. Fish. Aquat. Sci. 50:1343–1345.

Pepin, P., T. H. Shears, and Y. de Lafontaine.
1992. Significance of body size to the interaction between a larval fish (*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). Mar. Ecol. Prog. Ser. 81:1–12.

Rice, J. A., L. B. Crowder, and M. E. Holey.
1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. 116:703–718.

Rice, J. A, T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis.
1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. Can. J. Fish. Aquat. Sci. 50:133–142.

Ricklefs, R. E.
1973. Patterns of growth in birds. II: Growth rate and mode of development. Ibis 115:177–201.
1979. Adaptation, constraint, and compromise in avian postnatal development. Biol. Rev. Camb. Philos. Soc. 54:269–290.

Rosenberg, A. A., and A. S. Haugen.
1982. Individual growth and size-selective mortality of larval turbot (*Scopthalmus maximus*) reared in enclosures. Mar. Biol. 72:73–77.

Seikai, T., J. B. Tanangonan, and M. Tanaka.
1986. Temperature influence on larval growth and metamorphosis of the Japanese flounder *Paralichthys olivaceus* in the laboratory. Bull. Jpn. Soc. Fish. 52:977–982.

Taggart, C. T., and K. T. Frank.
1990. Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships. *In* K. Sherman, L. M. Alexander. and B. D. Gold (eds.), Large marine ecosystem: patterns processes and yields, p. 151–164. Am. Assoc. Adv. Sci. Publ., Washington, D.C.

Travis, J.
1981. Control of larval growth variation in a population of *Pseudoacris triseriata* (Anura: Hylidae). Evolution 35:423–432.

Whiting, D. A. and K. W. Able.
1995. Predation by sevenspine shrimp *Crangon septemspinosa* on winter flounder *Pleuronectes americanus* during settlement: laboratory observations. Mar. Ecol. Prog. Ser. 123:23–31.

Wilkinson, L.
1990. Systat: the system for statistics. Evanson, IL, 677 p.

Zar, J. H.
1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Int, Inc., Englewood Cliffs, NJ, 718 p.

Archeological evidence of large northern bluefin tuna, *Thunnus thynnus*, in coastal waters of British Columbia and northern Washington

Susan Janet Crockford

Pacific Identifications
6011 Oldfield Rd., RR #3, Victoria, British Columbia, Canada V8X 3X1
E-mail address: c/o anthuvic@uvvm.uvic.ca

Abstract.—This study presents archeological evidence for the presence of adult bluefin tuna, *Thunnus thynnus*, in waters off the west coast of British Columbia and northern Washington State for the past 5,000 years. Skeletal remains of large bluefin tuna have been recovered from 13 archeological sites between the southern Queen Charlotte Islands, British Columbia, and Cape Flattery, Washington, the majority found on the west coast of Vancouver Island.

Vertebrae from at least 45 fish from 8 sites were analyzed. Regression analysis (based on the measurement and analysis of modern skeletal specimens) was used to estimate fork lengths of the fish when alive; corresponding weight and age estimates were derived from published sources. Results indicate that bluefin tuna between at least 120 and 240 cm total length (TL) (45–290 kg) were successfully harvested by aboriginal hunters: 83% of these were 160 cm TL or longer. Archeological evidence is augmented by the oral accounts of native aboriginal elders who have described strategies used until the late 19th century for hunting bluefin tuna.

Despite this information, there are no 20th-century records of adult bluefin tuna in the northeastern Pacific. Archeological evidence suggests that either perturbations in the distribution of Pacific bluefin have occurred relatively recently or the specific environmental conditions favoring the movement of large tuna into northeastern Pacific waters have not occurred in this century.

Manuscript accepted 4 September 1996.
Fishery Bulletin 95:11–24 (1997).

Evidence is presented here for the occurrence of adult bluefin tuna, *Thunnus thynnus*, in waters of the northeastern Pacific, off the coast of British Columbia and northern Washington, for the past 5,000 years. The physical evidence consists of archeological remains of large bluefin tuna harvested by aboriginal hunters. Aboriginal North Americans of this area (part of the so-called "Northwest Coast" culture region) were accomplished seamen and skilled hunters of marine mammals (Mitchell and Donald, 1988). Coastal archeological sites throughout this region often contain abundant skeletal remains of the many fish and marine mammal species that sustained human populations over thousands of years (Calvert, 1980; Huelsbeck, 1983; Mitchell, 1988).

Skeletal remains of large bluefin tuna have been recovered from 13 archeological sites. The archeological deposits containing tuna date from at least 5,000 years ago until the early 20th century. The existence of bluefin tuna remains from this region have been previously reported (McMillan, 1979), but none were systematically analyzed until now.

For this study, 78 intact vertebrae from 8 archeological sites were measured and the data compared with those from vertebrae of modern specimens (specimens from the remaining 5 sites could not be examined, owing largely to difficulties in retrieving archived specimens but, in one case, because all skeletal material had been discarded by museum staff). Tentative estimates of the size of the archeological specimens were made by comparing the size of vertebrae from modern specimens of known length with the size of vertebrae collected from archeological deposits. The resulting length estimates were then used to calculate weight and age estimates by using length–weight algorithms derived from recent data. Data are presented in a manner that should facilitate the analysis of any additional archeological specimens recovered.

In addition to the results of the analysis of the archeological material, anecdotal evidence is presented from ethnographic accounts of tuna-fishing methods related by native elders of the Mowachaht tribe who live on the west coast of Vancouver Island. These recent oral accounts substantiate and augment the physical evidence: they describe bluefin tuna ethology, pinpoint the time of year that bluefin tuna were present and confirm that large bluefin tuna were being harvested in the northeastern Pacific until the late 19th century. The historic evidence for bluefin tuna occurrence in this area, although sparse, is also presented.

The archeological evidence and ethnohistoric accounts are significant because of the absence of modern records for adult bluefin tuna in the northeastern Pacific. Consequently, the distribution of northern bluefin tuna of all age classes in the Pacific and all modern records for adults in the eastern Pacific are reviewed. The addition of historical information presented here to our present state of knowledge of modern bluefin tuna distributions has important implications for our understanding of changing environmental conditions over time and perhaps also for determining the impact of 20th-century fisheries on Pacific bluefin tuna populations.

Distribution of Pacific bluefin tuna

The distribution of northern bluefin tuna in the Pacific is somewhat enigmatic, especially that of the adult portion of the population (Foreman and Ishizuka, 1990; Bayliff, 1994; Smith et al., 1994). Sexual maturity in Pacific northern bluefin is reached at about 5 years, and most spawning is reported between April and July in waters off Japan and the Philippine Islands, and in August in the Sea of Japan (Bayliff, 1994). Northern bluefin tuna are transoceanic migrators in both the Atlantic and Pacific; the movements of these fish are largely deduced by tagging experiments and catches of various age classes at specific times and locations (Nakamura, 1969; Rivas, 1978; Bayliff, 1994).

Some of the population of Pacific bluefin tuna migrate from the western to the eastern Pacific Ocean during their first or second year. The proportion of the population that undertakes this migration appears to vary from year to year (Bayliff et al., 1991). These migrating fish spend a period of one to six years in the eastern Pacific, a sojourn which may or may not be interrupted by visits to the central or western Pacific before the survivors return to spawn in the west (Bayliff, 1994). Adult fish in the Pacific appear to follow a general pattern of being distributed farther to the west during the spring (when spawning occurs) and farther to the east in the fall (Bayliff, 1993).

It is not known if all fish return to spawn every year after sexual maturity is reached. Tagging experiments indicate that although the journey from west to east may take 7 months or less, the journey from east to west takes nearly 2 years; therefore there does not appear to be enough time for mature adult fish migrating from the eastern Pacific to spawn in the west every year. In addition, because a few adult fish have been captured in the eastern Pacific either just before or after the spawning season, some adults probably do not return to the western Pacific every year but rather spend variable lengths of time in the eastern Pacific (Bayliff, 1994).

Most harvested adult bluefin tuna are caught in the western Pacific, where they are known to range as far north as the Sea of Okhotsk at about 50°N (Bayliff, 1980). Catch records of large bluefin tuna are noted at feeding areas off northeastern Honshu, Japan (ca. 40°N), off eastern Taiwan (about 25°N), and in the central Pacific near the Emperor Seamount (40°N, 175°E) (Nakamura, 1969).

Adult bluefin tuna are considered rare everywhere in the eastern Pacific; sporadic records have come from southern California and northern Mexico only. Although small bluefin tuna (less than 120 cm total length [TL] and 5–45 kg) are caught regularly off California and Mexico and somewhat larger fish (120–160 cm TL and 45–80 kg) occasionally, adults over 160 cm TL (80 kg) are seldom encountered (Foreman and Ishizuka, 1990; Bayliff, 1994).

In the northern portion of the eastern Pacific, few modern records exist for bluefin tuna. Neave (1959) mentioned three occurrences in British Columbia waters during August 1957 and 1958, but no sizes or numbers were given. These reports came from an area approximately 200–400 miles off the west coast of Vancouver Island (49°N, 134°24'W; 48°N, 131°06'W; 51°N, 130°W). A 7.5-kg bluefin tuna was caught in a salmon seine in July 1958, near Kodiak, Alaska, and on 1 October 1957, bluefin tuna were sighted 80–100 miles off Cape Flattery, Washington (Radovich, 1961). Sea-surface temperatures off the British Columbia coast were reported as being warmer than usual during both years.

I presume (because no sizes are mentioned in the reports) that these recent northern records are for relatively small fish of 5–45 kg because this size range is the most common in the eastern Pacific. Bluefin tuna larger than 45 kg in the eastern Pacific are rare enough that they are noteworthy when encountered. Although the earliest modern record of a very large bluefin tuna in southern California appears to be that of 1899 (Holder, 1913), sporadic occurrences of bluefin tuna over 50 kg have been reported since then (Dotson and Graves, 1984; Foreman and Ishizuka, 1990).

The largest reported catch of giant bluefin tuna in the eastern Pacific was made in 1988 (Foreman and Ishizuka, 1990). Seiners caught an estimated 987 adult bluefin tuna between November and early January off southern California, including many over 100 kg and some more than 250 kg, including one that broke California records at 458 kg and 271.2 cm TL. Seiner operators involved in this fishery reported that large bluefin tuna travelled in small

schools of less than 10 similar-size individuals, often less than 5 for very large fish.

Analysis of stomach contents of some of these fish indicated that they had been feeding at the surface on chub mackerel, *Scomber japonicus,* and the opalescent inshore squid, *Loligo opalescens,* a strongly phototactic species (Recksiek and Frey, 1978). Bluefin tuna are also reported to be phototactic (Bayliff, 1980). When water temperatures were recorded for these 1988 catches, they indicated lower than average sea-surface temperatures (mean 14.1°C) for southern California waters in the eastern Pacific. Bluefin tuna are generally found associated with water temperatures of 17–23°C (Bell, 1963).

The commercial catch of such high numbers of large fish in 1988 has raised the possibility that adult bluefin tuna may occur regularly off California but are only occasionally recognized or observed. Foreman and Ishizuka (1990) have suggested that small schools of adult bluefin tuna may go unrecognized if mistaken for pods of marine mammals or go undetected if travelling or feeding at depth. If so, it may be that the conditions that govern their infrequent movement into inshore feeding areas are very specific and thus rarely occur.

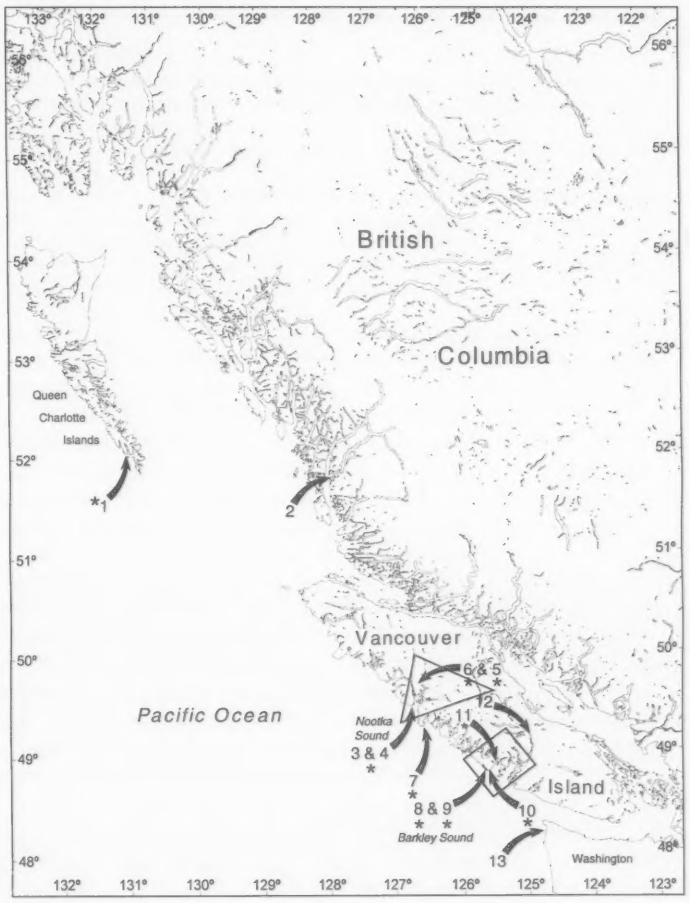


Figure 1

Map of the Pacific northwest coast of North America, showing the location of archeological sites from which bluefin tuna, *Thunnus thynnus,* remains have been recovered. *indicates samples examined in this study. *1 = FaTt 9 Louscoone Point; 2 = ElSx 1 Namu; 3 = DjSp 1 Yuquot village; *4 = DjSp 3 Yuquot midden; *5 = DkSp 1 Kupti; *6 = DkSp 3 Tahsis midden; *7 = DiSo 1 Hesquiat; 8 = DfSi 4 Macoah; * 9 = DfSi 5 Ch'uumat'a; *10 = DfSj 23A T'ukw'aa village; *11 = DfSj 23B T'ukw'aa defensive site; 12 = DhSe 2 Shoemaker Bay; 13 = 45CA24 Ozette village.

Analyses and results

The archeological sample

Vertebrae were examined from 8 of the 13 sites from which remains of bluefin tuna were found. As is typical for faunal remains recovered from archeological sites, chronological dates for tuna specimens are estimated in relation to the ^{14}C-dated strata from which they were recovered: none of the bluefin tuna remains have yet been dated directly.

The northernmost archeological evidence for the occurrence of bluefin tuna is from the southern Queen Charlotte Islands (Fig. 1), whereas Namu on the central British Columbia mainland is the oldest known deposit yielding bluefin tuna remains (dated at 4050–3050 BC). Bluefin tuna have also been recovered from sites at Hesquiat Harbour and Shoemaker Bay on the west coast of Vancouver Island and from the Ozette site near Cape Flattery, Washington (see Table 1 for more details). Vertebrae are the only traces of bluefin tuna recovered from the above sites, and only specimens from the Hesquiat Harbour and Queen Charlotte Islands were available for analysis.

Archeological excavations at four sites each in both Nootka and Barkley Sounds on the west coast of Vancouver Island also yielded bluefin tuna remains and, in contrast to other area sites, both vertebral and nonvertebral skeletal remains are represented. Neither scales nor otoliths, however, were found. Tuna were reported from all strata of the 1966 excavation at the village of Yuquot on Nootka Sound

Table 1

Archeological sites from which bluefin tuna, *Thunnus thynnus*, remains have been recovered, with excavation information, dates, references and numbers of remains reported that could not be analyzed in this study.

Area and site no.	Description of site and excavated remains
Queen Charlotte Islands and the North Coast, British Columbia	
1 (FaTt 9)	Louscoone Point village, Kunghit Haida territory; 52°08'N, 131°14'W; small test excavation 1985 (Wigen[1];Acheson[2]); from deposits dated ca. AD 800–ca.1800.
2 (ElSx 1)	Namu village, Bella Bella territory; 51°52'N, 127°52'W; major excavation 1969–71; from deposits dated 4050–3050 BC (Cannon, 1991); 1 vertebra reported.
Vancouver Island, British Columbia	
Nookta Sound area sites, Mowachat territory; ca. 49°40'N, 126°37'W	
3 (DjSp 1)	Yuquot village; major 1966 excavation; from all deposits 2300 BC– AD 1880 (McMillan, 1979); 87 vertebral and nonvertebral specimens reported.
4 (DjSp 3)	Yuquot fishing station; from surface collection 1968;no dates (Marshall[3]).
5 (DkSp 1)	Kupti village; small 1968 excavation; from deposits ca. AD 1260–1460 (Marshall[3]).
6 (DkSp 3)	Tahsis Inlet midden; from 1990 shovel test; no dates (Marshall[3]).
7 (DiSo 1)	Hesquiat village, Hesquiat territory; 49°24'N, 126°28'W; major 1973–75 excavation; from deposits dated AD 1230–1430 (Calvert, 1980).
Barkley Sound area sites, Toquat territory; ca. 49°N, 125°20'W; 1991–93 excavations (McMillan and St. Claire[4])	
8 (DfSi 4)	Macoah village; bluefin from upper levels of deposits dated 2460 BC–ca.AD 1880.
9 (DfSi 5)	Ch'uumat'a village; bluefin from deposits dated ca. AD 1370.
10 (DfSj 23A)	T'ukw'aa village; bluefin tuna from deposits dated AD 760–1310.
11 (DfSj 23B)	T'ukw'aa defensive site; bluefin tuna from deposits dated AD 1175–1880 .
12 (DhSe 2)	Shoemaker Bay, Tseshaht territory; 49°15'N, 124°49'W; major 1973/74 excavation; from deposits dated AD 500–820 (Calvert and Crockford, 1982); 17 vertebrae reported.
Olympic Peninsula, Washington State	
13 (45CA24)	Ozette village, Cape Alava; Makah (Nuu-chah-nulth subdivision) territory; 48°10'N; 124°44'W; major 1971–80 excavation; from house floor deposits dated AD 1510 (Huelsbeck, 1983); 2 vertebrae reported (one modified).

[1] Wigen, R. J. 1990. Identification and analysis of vertebrae fauna from eighteen archaeological sites on the southern Queen Charlotte Islands. British Columbia Heritage Trust, 800 Johnson St. Victoria, British Columbia, Canada V8W 1N3. Unpubl. rep., 79 p.
[2] Acheson, S. 1992. Archaeology Branch, British Columbia Ministry of Small Business, Tourism, and Culture, 800 Johnson St., Victoria, British Columbia, Canada V8W 1N3. Personal commun.
[3] Marshall, Y. M. 1990. The Mowachaht archaeology project, phase 1, 1989. Archaeology Branch, British Columbia Ministry of Small Business, Tourism, and Culture, 800 Johnson St., Victoria, B.C., Canada V8W 1N3.
[4] See Footnote 3 in the main text of this paper.

(dated from about 2300 BC to ca. AD 1880), making this the longest continuous record of *Thunnus* occurrence in the region (McMillan, 1979; Marshall, 1993). Unfortunately, these specimens are archived in Ottawa and could not be retrieved easily for analysis: three other small excavations undertaken during 1968 and 1990 at sites along Nootka Sound, however, recovered remains of bluefin tuna and these specimens were available for inclusion in this analysis.

It is pertinent to mention that all fish remains from the 1966 excavation of the village at Yuquot were identified to genus level only (McMillan, 1979), perhaps giving the impression that the tuna remains might be albacore *(T. alalunga)*, a species that occurs regularly in the eastern Pacific (Hart, 1973). However, crew working on the excavation of Yuquot reported that remains of some very large fish were recovered (Dewhirst[1]). According to the literature (and in my own twenty years experience analyzing faunal remains from this area), albacore have never been reported from any archeological site in British Columbia. Moreover, albacore rarely, if ever, exceed 50 kg; it therefore seems unlikely that *Thunnus* remains from Yuquot are albacore rather than bluefin tuna.

[1] Dewhirst, J. 1992. Archeo Tech Associates, 1114 Langley St., Victoria, British Columbia, Canada V8W 1W1. Personal commun.

Table 2

Calculated fork lengths (cm) and estimated weights (kg) of comparative specimens—USNM catalog numbers 269001, 269004, 268964, 269002 (Nankai collection numbers 1, 2, 3, 6) National Museum of Natural History (NMNH), Smithsonian Institution.

	Nankai 1 269001	Nankai 2 269004	Nankai 3 268964	Nankai 6 269002
Skull length (cm)	26.2	25.3	23.5	28.5
Total of vertebral lengths (1–39 cm)[1]	148.1	124.1	121.2	146.9
Total skeletal length (SL) (cm)	174.3	149.4	144.7	175.4
Estimate of intervertebral cartilage—40 spaces	20.0	20.0	20.0	20.0
Estimate of snout and tail flesh (cm)	10.0	10.0	10.0	10.0
Estimated fork length (cm)	204.3	179.4	174.7	205.4
Estimated weight (kg)[2]	184	130	121	187

[1] All measurements available from the author or NMNH, Smithsonian Institution.
[2] Foreman and Ishizuka, 1990; 184.

Recent excavations at four locations along Toquart Bay in Barkley Sound on the west coast of Vancouver Island have recovered relatively large numbers of both vertebral and nonvertebral bluefin tuna skeletal remains. Full analysis of this material is still in progress: only a few of the nonvertebral remains have been examined thus far. All vertebrae, however, are included in this study.

Modern skeletal samples

In order to estimate the size of fish represented by isolated vertebrae from archeological samples, it was necessary to determine the size relationship between individual vertebrae and the corresponding fork length in modern samples of the fish. Measurements taken from the vertebrae of modern skeletal specimens of known-size fish of comparable size were used for this purpose (Casteel, 1976; Wheeler and Jones, 1989).

Recent skeletal specimens of large (160 cm TL and over) Pacific bluefin tuna were found to be extremely rare, and the only known specimens had, unfortunately, no corresponding size data (length or weight); therefore fork lengths (snout to fork of the tail) had to be estimated for these specimens as well. Fortunately, these four recent specimens of bluefin tuna (loaned by B. Collette, Museum of Natural History, Smithsonian Institution, Washington, D.C.) have skulls that are still articulated, and it was possible to determine a "skeletal length" for these specimens (Table 2). The skeletal length is defined as the basal length of the skull plus the combined lengths of all 39 vertebrae. The vertebral column of the comparative specimens had been sawed into sections during skeletal preparation, sometimes by cutting through a centrum. Vertebra no. 30, either by itself or with portions of no. 29 and no. 31 attached, was apparently removed from the specimens at some point and not returned. Estimates of the length measurements of all three of these vertebrae were used in the regression equations. These four fish appear to be the only disarticulated skeletal specimens of large Pacific bluefin tuna available for analysis (however, several museums have reconstructed skeletal specimens of large individuals on display). All raw data for these specimens are available on request from the author and are also on file at the National Museum of Natural History, Smithsonian Institution.

In order to estimate a fork length from the skeletal length for these comparative specimens, I assigned a value of 0.5 cm to the intervertebral cartilage (40 spaces, 20 cm total) and an additional 5 cm each for flesh on the snout and the tail. These values consistently added 30 cm to the measured skeletal length and yielded an estimated fork length. This method was chosen so that if a more accurate determination of the "soft tissue" component of the fork length of bluefin tuna is subsequently developed, the estimates given in this report can be easily adjusted.

The vertebral centrum length and breadth measurements from the four comparative specimens (Fig. 2) were used in single (least-squares) regression equations for each of the 39 vertebrae in the spinal column by using logarithmic transformations of vertebral and skeletal length measurements to determine their linear relationship. Because the size and shape of vertebrae change (sometimes quite dramatically) over the length of the fish, it was necessary to calculate a separate algorithm for each vertebra in the spinal column.

Table 3 presents the resulting values for the relationship between the greatest centrum length, GL, and greatest proximal centrum breadth, GB(p), to the skeletal length, SL, for the recent specimens as calculated by regression analysis. In this table, some values are missing or are based on only 3 specimens owing to the original preparation of the comparative skeletons. Standard deviations and confidence limits are not given but are available on request.

Size determination of archeological specimens

The standard formula used to estimate the size of fish represented by the archeological specimens is given by Casteel (1976, p. 96) as: log (*fork length*) = $a + b \times \log$ (*GL* or *GB*). The constant (a) and the slope—or x coefficient —(b) are taken from Table 3 (i.e. the values derived from the comparative specimens), and the logarithm of the greatest length, *GL*, or proximal breadth, *GB(p)*, from each archeological specimen (Table 4).

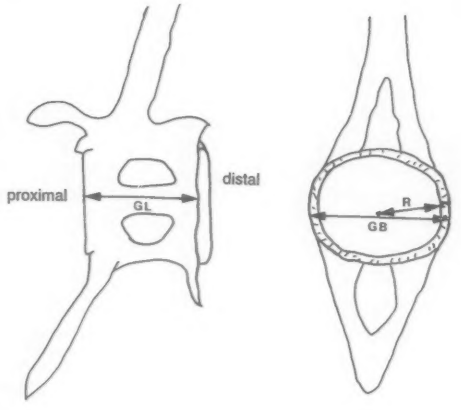


Figure 2

Definitions of vertebral measurements taken from both comparative and archeological specimens of bluefin tuna. Greatest length (GL): maximum length of the centrum, taken at the lateral midpoint with digital calipers and measured to the nearest mm. Greatest breadth (GB) = maximum breadth of the centrum, taken at the lateral midpoint of the proximal face, GB(p), and distal face, GB(d), taken with digital calipers and measured to the nearest mm. Radius (R) = the maximum distance from the center of the cone to the edge, of the proximal face, R(p), and distal face, R(d), taken at the lateral midpoint. This measurement was taken with a plastic ruler cut diagonally to fit into the cone of the centrum; in this way the amount of growth from the center of the cone to the sharp raised ridge at the lip of the centrum was measured to the nearest 0.5 mm.

Casteel (1976) noted that although the regression method is the most accurate way to estimate fish length from bone size, these length estimates always vary somewhat between vertebrae from the same individual, even when the predictive value (r) of the equation is high. When both length and breadth measurements were available for an archeological specimen, the measurement that produced the length estimate with the highest correlation coefficient (r) value for that individual was used to represent that fish. Alternatively, an average of all available measurements could have been made, although this method allowed both comparative and archeological specimens to be treated similarly.

The method used in the present study required that vertebral specimens be identified to exact column position. This can be problematic for archeological specimens because several of the centra in the vertebral column are almost identical and because archeological specimens may often lack diagnostic neural or haemal arches and spines. However, an archeological specimen can almost always be defined to a small range within the column (e.g. vertebrae numbers 14–16). Vertebrae not identified to exact position were found to be so similar in size and proportion to adjacent vertebrae that they could be treated as interchangeable for the purpose of the estimations attempted here. Where the exact position of an archeological specimen was uncertain (which occurred for less than one third of the specimens examined), the number of the vertebra used to calculate the size estimates is given in parentheses, e.g. (15).

Table 4 presents all archeological vertebrae measured (by vertebra number) and the length estimates derived from them. Where eroded edges prevented accurate measurement, an estimate was taken if it was likely to be accurate to within 1 mm. A total of 78 vertebrae were measured, representing at least 45 individuals. Several vertebrae were found attached (occasionally in articulated position) or could potentially have belonged to the same individual by virtue of similar size and proximity within the archeological deposit (this is a standard assumption for determining the minimum number of individuals represented by skeletal remains recovered from archeological contexts). Radius measurements of these specimens were also taken (because this dimension is preferred by some researchers for ageing purposes) but are not reported or used in the calculations. All measurements are available on request from the author.

The fork-length estimates for the archeological sample listed in Table 4, as for the comparative skeletons, are derived by adding 30 cm to the estimated skeletal length to yield a fork length (to account for

Table 3

Regression analysis values: log of vertebral lengths, *GL*, and proximal breadth, *GB(p)*, vs. log of skeletal length, *SL*, of 4 modern bluefin specimens (USNM 269001, 269004, 268964, 269002). NA = not applicable. Number of observations=4 (*=3); Degrees of freedom=2 (*=1).

Vertebra no.	Constant *GL*	X Coefficient *GL*	*r* value *GL*	Constant *GB(p)*	*X* Coefficient *GB(p)*	*r* value *GB(p)*
1	4.8553	0.7814	0.903	NA	NA	NA
2	4.6692	0.8328	0.881	3.8396	0.9154	0.892
3	4.4210	0.9155	0.917	4.0180	0.8634	0.945
4	4.6286	0.8486	0.901	4.4710	0.7433	0.965
5	5.2932	0.6351	0.908	4.5377	0.7295	0.997
6	4.9966	0.7257	0.933	4.6478	0.7096	0.981
7	4.2052	0.9593	0.992	4.3649	0.8043	0.970
8	4.1994	0.9492	0.932	4.0022	0.9111	0.970
9	4.6598	0.8064	0.955	3.9509	0.9272	0.985
10	4.7950	0.7543	0.928	3.9373	0.9300	0.994
11	3.9914	0.9810	0.993	3.8234	0.9561	0.996
12	5.3210	0.5964	0.908	4.2293	0.8463	0.985
13	4.6473	0.7785	0.971	4.3599	0.8081	0.994
14	4.4486	0.8287	0.983	4.0404	0.8918	0.992
15	4.5968	0.7815	0.954	4.4404	0.7807	0.988
16	4.6118	0.7746	0.991	4.4515	0.7768	0.986
17	4.2226	0.8808	0.972	4.3918	0.7903	0.989
18	3.5879	1.0526	0.962	4.3059*	0.8088*	1.000
19	4.3551	0.8328	0.997	4.2695	0.8175	0.988
20	4.3449	0.8360	0.994	4.4124	0.7797	0.983
21	4.1621	0.8809	0.985	4.3422	0.7963	0.987
22	4.2308	0.8604	0.987	4.2783	0.8129	0.991
23	5.1630*	0.5922*	0.705	NA	NA	NA
24	4.3756	0.8189	0.987	4.4521	0.7663	0.989
25	4.2320	0.8561	0.989	4.1347	0.8494	0.988
26	4.0288	0.9085	0.997	4.2699	0.8127	0.975
27	3.8883	0.9387	0.995	4.4668	0.7626	0.984
28	3.8464	0.9475	0.996	3.9946	0.8854	0.993
29	3.4217	1.0551	0.976	4.1875	0.8305	0.979
30	4.0737	0.8741	0.937	4.1472	0.8386	0.999
31	3.6730	0.9715	0.886	NA	NA	NA
32	4.0061	0.8852	0.876	NA	NA	NA
33	4.5576	0.7398	0.859	3.7206	0.9430	0.995
34	5.1867	0.5850	0.598	3.9220	0.9076	0.998
35	5.6621	0.4777	0.595	4.3345	0.8317	0.976
36	5.3978	0.5952	0.942	5.8817*	0.4347*	0.713
37	5.7937	0.6068	0.921	3.5138	1.1630	0.990
38	6.2246	0.5138	0.862	3.1768	1.3458	0.988
39	3.7247	0.9270	0.901	4.5084	0.9313	1.000

intervertebral cartilage [20 cm] and flesh on the snout and tail [10 cm]). Weight estimates have been calculated from the formula derived by Foreman and Ishizuka (1990) for large Pacific bluefin and are presented in Table 5.

Age estimations included in Tables 5 and 6 are compiled from data presented by Bayliff (1994) that was based on fork-length estimates. However, Hales and Reitz (1992) cautioned that age data determined from modern population samples may differ from prehistoric populations. They report a distinct change in growth rates over time for Atlantic croaker, *Micropogonias undulatus* (Perciformes: Sciaenidae), from Florida, a change determined from the analysis of otolith growth increments from prehistoric samples. Compared with modern populations, croakers from populations of several centuries ago grew more slowly and lived much longer.

Although the results of the croaker study suggest that modern data relating size to age may not accurately predict the age of prehistoric fish specimens, no data are currently available to address this phenomenon for any population of bluefin tuna. Should bluefin tuna be shown to exhibit the same pattern as croaker, the archeological specimens of bluefin tuna reported here would actually represent fish older than those predicted by this analysis. However, length measurements were converted to age and weight estimates in this study primarily so that comparisons could be made with modern tuna distribution data, which are often reported by age class or weight. The critical point was to establish whether adult, rather than juvenile, tuna were more abundant in the archeological sample, because these age classes display distinctive behaviors and, more importantly, have different ecological requirements.

Size of bluefin tuna represented by the archeological sample

Table 5 presents the final length, weight, and age estimates of bluefin tuna by geographic area. By far the majority of fish within the total sample (83%) were at least 6 years or older, ranging between 160

Table 4

Archaeological bluefin tuna vertebrae measurements and fork length estimates, by vertebrae number. All specimens. Measurements are defined in Figure 2.

Vertebra no.	Centrum GL (mm)	Centrum GB(p) (mm)	Estimated FL (cm)	Vertebra no.	Centrum GL (mm)	Centrum GB(p) (mm)	Estimated FL (cm)
01	27.0	44.4	198.7	21	38.3	45.1	189.6
02	26.3	48.2	191.5	22	39.2	44.8	189.6
04	22.5	39.6	164.7	22	39.2	46.5	188.6
04	31.6	65.1	224.9	24	39.4	47.5	193.5
05	27.1	58.7	212.4	24	45.1		195.3
06	30.8	58.9	218.2	25	40.8	48.3	209.8
09	25.6	34.4	168.2	26	40.1	47.6	194.8
(09)		48.7	220.8	(28)	30.2	35.9	190.7
(09)	22.3	30.5	153.6	29	33.7	36.3	159.3
(10)	33.4	45.0	206.7	29	45.3	49.5	155.3
11	24.4	34.6	165.5	29	50.3	58.2	201.1
(11)	31.0	37.8	177.5	30	28.1	32.0	221.1
(12)	35.0		200.5	30	36.7		138.5
(12)	36.7	46.5	206.9	30	38.3	44.0	167.1
(12)	34.9	41.9	192.0	30	46.7		172.3
14	33.5		187.0	30	47.3	50.0	199.2
(14)	33.9	40.9	185.4	30	47.5	51.2	201.1
(14)	34.1	42.0	189.3	31	48.6	52.8	201.7
(14)	32.5	42.1	189.7	31	52.7	53.8	201.3
(14)	27.7	32.8	157.8	32	41.7	45.6	215.3
15	35.4	42.5	188.4	32	43.7		179.3
(15)	31.4	42.5	188.4	32	49.7	54.4	185.6
16	35.9	45.6	191.2	33	26.6	27.0	204.4
16	36.1	42.9	191.9	33	43.8	44.8	122.4
(16)	31.3	35.4	175.0	33	44.5	47.2	178.9
(16)	33.8	40.9	183.9	33	44.7	45.6	186.5
(16)	40.2	47.2	206.0	33	47.9	53.9	181.4
(16)	41.2	51.8	209.4	33	52.2	53.7	207.3
17	36.0	42.8	187.3	33	53.7	55.2	206.7
17	37.5	47.3	200.2	34	48.1		211.3
(17)	37.0	43.9	190.4	34	48.2		202.4
(17)	38.2	44.2	191.3	35	41.2	42.0	202.6
18	37.2	46.5	195.4	36	30.5		200.8
(18)	26.8	32.4	153.5	38	11.9	28.2	198.9
19	39.4	47.2	196.0	38	16.5	31.8	210.3
(19)	27.2	32.7	151.9	39		23.0	243.2
20	35.5	44.5	182.4	39		19.5	198.3
(20)	38.0	45.0	191.3				
(20)	44.3	54.0	213.4				

Table 5

Archeological bluefin tuna length and age estimates, per individual represented, listed by geographic area. The length estimate associated with the highest correlation coefficient (r) for individuals represented by several elements is used here. See Figure 1 for locations.

Specimen no.	Site no.	Vertebra no.	Estimated fork length[1] (cm)	Estimated weight[2] (kg)	Estimated age class[3] (yr)
Barkley Sound, Vancouver Island, n = 36					
52	DfSi5	33	122.4	47	4
84	DfSj23a	30	138.5	65	5
51	DfSi5	(19)	151.9	83	5–6
54	DfSj23a	(18)	153.5	86	5–6
59	DfSj23a	29	155.3	88	5–6
30	DfSj23a	(14)	157.8	92	5–6
58	DfSj23a	11	165.5	105	6
25	DfSi5	30	167.1	107	6
55	DfSj23a	09	168.2	109	6
85	DfSj23a	30	172.3	117	6–7
83	DfSj23a	(16)	175.0	122	6–7
49	DfSi4	33	178.9	129	6–7
56	DfSj23a	33	181.4	134	7
48	DfSj23a	(16)	183.9	139	7
61	DfSj23a	33	186.5	144	7
39E	DfSi4	17	187.3	146	7
36C	DfSi4	22	188.6	149	7
47	DfSi4	(14)	189.3	150	7
60	DfSj23a	(14)	189.7	151	7
69F	DfSj23b	26	190.7	153	7
86	DfSi4	(20)	191.3	154	7
87	DfSj23a	02	191.5	155	7
57	DfSi5	01	198.7	171	7–8
26	DfSj23b	(12)	200.5	175	7–8
32	DfSi4	30	201.1	176	7–8
24	DfSj23a	(16)	206.0	188	8
44	DfSj23a	33	206.7	190	8
31	DfSj23a	(12)	206.9	190	8
68	DfSj23a	(16)	209.4	197	8
45A	DfSi4	24	209.8	198	8
64	DfSj23a	05	212.4	204	8
67	DfSj23b	31	215.3	212	8
63	DfSi4	06	218.2	219	8
72	DfSi4	(09)	220.8	226	8–9
66	DfSi4	29	221.1	227	8–9
80	DfSj23a	38	243.2	293	9–10
Hesquiat Harbour, Vancouver Island, n = 2					
21	DiSo1	32	186.0	143	7
20	DiSo1	(20)	213.4	207	8
Nootka Sound, Vancouver Island, n = 6					
NA	DkSp1	(28)	159.0	94	5–6
NA	DkSp1	(11)	177.0	125	6–7
1	DjSp3	39	198.3	170	7–8
3E	DkSp1	36	198.9	171	7–8
4	DkSp1	(10)	206.7	190	8
2	DkSp1	38	210.3	199	8
Queen Charlotte Islands, n = 1					
15E	FaTt9	19	196.0	165	7–8

[1] All raw data and calculations available from the author.
[2] Log (weight, kg) = (–9.02408) + 2.6767 × log (length, cm) (Foreman and Ishizuka, 1990).
[3] After Bayliff 1994a: 246.

Table 6

Distribution of estimated age and size classes of bluefin tuna harvested within the Barkley Sound area only, based on archeological remains from Barkley Sound area sites.

Estimated fork length (cm)	Number of individuals	Estimated age class (yr)[1]
120–129	1	4
130–159	5	5–6
160–179	8	6–7
180–199	11	7–8
200–219	8	8
220–239	2	8–9
240–260	1	9–10
	Total = 36	

[1] After Bayliff, 1994a: 246 (data for vertebrae only).

and 240 cm TL and between approximately 96 to 293 kg in weight. The youngest fish was estimated at 4 years (120 cm TL) and the oldest between 9 and 10 years (240 cm TL). Of the total sample of 45 individuals, 36 were recovered from the Barkley Sound area on the southwest coast of Vancouver Island, and the range of sizes from that area is summarized in Table 6. The relative size range of the bluefin tuna vertebrae harvested from Barkley Sound is shown pictorally in Figure 3.

Ethnographic and historic information

Information from ethnographic sources substantiates and augments archeological evidence indicating that large bluefin tuna were present and harvested by Nuu-chah-nulth people of Vancouver Island well into the 19th century. Elders of the Mowachaht group from Nootka Sound on Vancouver Island have contributed invaluable details about tuna hunting strategies employed by their elders, some through interviews with Richard Inglis of the Royal British Columbia Museum, Victoria, British Columbia during 1991 and 1992 (Inglis[2]). These accounts represent the only ethnographic description of aboriginal tuna hunting on the northwest coast (McMillan, 1979). Pertinent details that substantiate the occurrence of adult bluefin tuna during the historic period are presented here.

The month of August is said to have been the time when tuna could be found feeding at the surface in inshore waters (sea-surface temperatures during August usually average about 14°C [Sharp, 1978]). The occurrences of large tuna were apparently preceded and accompanied by recognizable changes in water and weather conditions and by a unique set of associated fauna. Tuna traveled well inside Nootka Sound into protected inlets and were harpooned at night as

[2] Inglis, R. 1993. British Columbia Ministry of Aboriginal Affairs, #100-1810 Blanchard St., Victoria, British Columbia, Canada V8V 1X4. Personal commun.

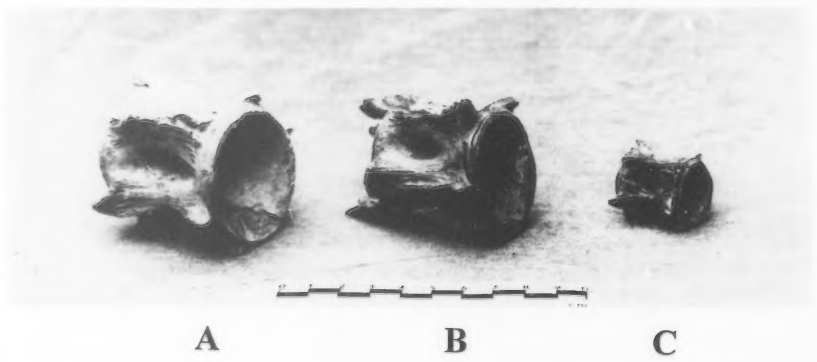


Figure 3

Selected vertebrae from Barkley Sound archeological deposits. See Figure 1 for locations. (**A**) Specimen no. 44, vertebra no. 33; site DfSj 23a; length ca. 210 cm; (**B**) Specimen no. 61, vertebra no. 33; site DfSj 23a; length ca. 190 cm; and (**C**) Specimen no. 52, vertebra no. 33; site DfSi 5; length ca. 120 cm.

they fed at the surface in shallow inshore waters (located by spotters positioned on nearby cliffs). Bioluminescent plankton present in the water made the big fish especially visible at night, even from a distance.

A fire was sometimes built in the bow of the hunter's canoe to attract the fish to within spearing distance, a strategy called "pit-lamping." Another method was to paddle the canoe quickly away from an area where tuna were spotted: the canoe created a path of light as it moved through the bioluminescence. The tuna would follow the light, right up to and under the canoe, and were harpooned as they emerged at the bow. The word for tuna ("silthkwa") means "like the bow wave made by a boat," and undoubtedly reflects their surface-feeding behavior. These tuna were always referred to as "big fish, 6 to 8 feet (ca. 180–244 cm TL) long."

George Louis of the Ahousat Band was about 80 years old when interviewed in 1992. He said that his father told a story about the tuna hunting he observed as a small boy (perhaps when about 10 years old) sometime between 1880 and 1890. No official records or unofficial accounts have been found which indicate that large tuna have been observed in British Columbia waters since that time. Large bluefin tuna were captured, however, by sport anglers during the 1890's in southern California (Holder, 1913).

The only written reference to tuna found to date in the historic record is a footnote in the account of a meeting between George Vancouver and Bodega y Quadra at Nootka Sound in 1792. Mention is made of a porpoise and tuna stew ("large Tunny and a Porpus") being served during a feast given in their honor by Nuu-chah-nulth chief Maquinna on 4 September 1792 (Lamb, 1984, p. 304). There is, of course, no way of knowing if the "tuna" was bluefin tuna, some other tuna species, or some other taxon altogether. The capture of porpoise, however, would have required similar hunting skills and equipment as those described above for bluefin, and both could have been caught during a single hunting expedition. "Porpoise" remains are reported from a number of coastal shell middens (Mitchell, 1988) and are most likely to be either harbour porpoise, *Phocoena phocoena*, white-sided dolphin, *Lagenorhyncus obliquidens*, or Dall's porpoise, *Phocoenoides dalli* (Leatherwood et al., 1988). Moreover, bluefin tuna (even very large ones) would have been quite familiar to the Europeans exploring the coastal waters of British Columbia because the similar Atlantic subspecies occurs in European coastal waters. In marked contrast to the many unknown species regularly encountered by explorers in the north Pacific, large bluefin tuna might have been so familiar that they did not warrant special comment.

Discussion

Archeological evidence and potential sampling bias

The archeological remains described above represent a size class of bluefin tuna previously unknown in the northern portion of the eastern Pacific and constitute a small but valuable biological sample of the ancient population. However, some of the cultural and taphonomic (postdepositional) influences that affected the sample must be considered before ecological or zoogeographic interpretations can be made.

The archeological shell middens from which the bluefin tuna specimens have been recovered are essentially garbage dumps created over many centuries by the disposal of food and other household waste. The calcium carbonate leaching from abundant shellfish remains in these midden deposits effectively neutralizes acids in the soils that would otherwise rapidly destroy bone. Preservation of vertebrate skeletal remains is often excellent under these conditions, even after several thousand years.

The bones of animals recovered during archeological excavation of a shell midden represent a very small portion of the animals harvested by aboriginal people. Many processes operate on the carcass of a harvested animal to reduce the number of bones that might eventually be discarded into a midden (Davis, 1987; Lyman, 1994). These include butchering methods, distribution of edible parts (sharing), cooking procedures, and consumption of the edible portions. Some bones may have been set aside for tool or ornament manufacture (only one piece of altered bluefin tuna has been recovered: a vertebra fashioned into a spool, from the Ozette Village site in Washington). Moreover, scavengers, especially dogs and birds, may have removed or destroyed parts of a carcass so that in the end only a few bones from any given animal are represented in the midden. Finally, only small portions of most large midden deposits are actually excavated by archeologists, further reducing the sample of harvested animals available for archeozoological analysis (Ringrose, 1993, for detailed discussions of these issues; Lyman, 1994). For example, the remains of the 36 individual bluefin tuna recovered from Barkley Sound (Table 6) represent an empirically undeterminable fraction of what was actually harvested and consumed by the aboriginal people in that area. In addition, the number of fish successfully landed constituted a very small proportion of the available population of bluefin tuna. Presumably only a few bluefin tuna would have been actively pursued and some of these would invariably have been lost during the hunt. Thus, even if only one gi-

ant bluefin tuna was successful harvested every few seasons by native hunters, this could still constitute evidence of a significant population of tuna available as a local resource.

Unfortunately, the time interval between catches of bluefin is not precisely determinable from the dated archeological deposits; it is impossible at this time to determine if catches were made annually, every 10 years, or every 100 years. Although expensive, the use of accelerator ^{14}C-dating methods on small samples of bluefin tuna remains is the only way to determine a more precise time frame. The remains of bluefin tuna recovered from Barkley Sound during several recent field seasons are perhaps the best candidates for future analysis because there are many vertebral and nonvertebral skeletal elements and the remains appear to represent less than 2,000 years of harvesting activities (McMillan and St. Claire[3]).

Geographic range of prehistoric bluefin tuna remains

As discussed at greater length previously (Crockford, 1994), it appears probable that the ability to hunt large Pacific bluefin tuna was strongly correlated with native groups who were capable of active whaling. This possible correlation with active whaling rather than with the use of so-called "drift" whales (which die naturally and are fortuitously encountered at sea or as beached carcasses) is important. No other archeological sites in western North America or northeastern Asia appear to contain remains of large bluefin tuna. No large bluefin tuna have been reported from sites in southern California where adult tuna are occasionally taken today, although the remains of other large fish, such as marlin, have been identified and large marine mammals, such as sea lions, were clearly taken (Moratto, 1984; Raab[4]). We cannot assume, however, that large bluefin tuna were not present in southern California waters during prehistoric times because a lack of whaling technology may have prevented aboriginal Californians from harvesting such a resource.

In northern Japan, active whaling is not clearly indicated by the archeological record although hunting of sea lions and other large marine mammals was practiced. Large bluefin tuna remains have not been reported from archeological sites bordering the Sea of Okhotsk and the Sea of Japan where large bluefin tuna occur today (Niimi, 1994; Otaishi, 1994), but it appears that not many large sites in these areas have been excavated. As in the case for California, it would be inappropriate, given the absence of evidence for an active whaling technology, to suggest that adult bluefin tuna were absent in Japanese waters during prehistoric times.

In contrast, the recovery of large bluefin tuna among dated archeological deposits that span almost 5,000 years is evidence that the occurrence of adult bluefin tuna off the British Columbia coast was longstanding. Clearly, large bluefin tuna were a resource consistently (if sporadically) available to aboriginal people on the central northwest coast until relatively recently. The Nuu-chah-nulth people, in particular, were especially adept at using this resource, and their material culture included large seagoing canoes, detachable harpoon heads, braided ropes, and floats required for the successful hunting of both whales and large tuna (Huelsbeck, 1983; Mitchell and Donald, 1988). Archeological remains are, by inference, invaluable indicators that the environmental conditions that favored the presence (i.e. the inshore surface-feeding behavior) of bluefin tuna must have existed off the coast of British Columbia as a recurring pattern for at least 5,000 years.

Implications

The lack of reports of adult bluefin tuna off the British Columbia coast since the late 19th century may be due to several factors, including the impact of 20th-century fisheries in both the eastern and western Pacific, the association of large bluefin in northern waters of the eastern Pacific with very specific environmental conditions that have not recurred since the late 19th century, and the misidentification of small schools of large bluefin tuna as marine mammals.

Although relative abundance records over the past 100–150 years are not available for Pacific bluefin tuna, it has been shown for other species that when abundance decreases, the range of a species often contracts (Kawasaki, 1991). In order to investigate how 20th-century fisheries may have impacted abundance and thus the distribution of bluefin tuna, a comprehensive record of the history of the bluefin tuna fishery as conducted by all nations throughout the north Pacific would be needed. This is especially true for Japanese waters because of the use there of large-scale harvesting methods.

It is also possible, however, that short- or long-term (or both) changes in environmental conditions may be affecting bluefin tuna distributions in the east-

[3] McMillan, A. D., and D. E. St. Claire. 1992. The Toquart archaeology project: report on the 1992 excavations. Archaeology Branch, British Columbia Ministry of Small Business, Tourism and Culture, 800 Johnson St. Victoria, British Columbia, Canada V8W 1N3: permit 1991–46. Unpubl. rep., 100 p.

[4] Raab, M. 1994. Anthropology Department, California State University, Northridge, CA 91330. Personal commun.

ern Pacific (Rothschild, 1991). Hubbs (1948) partially addressed this issue in his presentation of evidence that mean water temperatures in southern California were warmer in the mid-to-late 1800's (1850–80). Such water temperatures appeared to be associated with distinctly tropical fauna that no longer occur so far north. This period corresponds roughly to that mentioned in the northwest coast ethnographic accounts as the last time when large tuna were hunted and may reflect a recurring pattern of occasional warm periods along the whole coast of North America.

Because the surface-feeding behavior of large bluefin tuna makes them very conspicuous in inshore waters, it would be extremely unlikely for adult tuna to go totally unnoticed for the last 100 years in British Columbia waters (even if they could not be caught or were indeed mistaken for marine mammals in deeper waters). It seems reasonable to assume under the circumstances that modern records are correct: large adult bluefin tuna have not frequented the northern waters of the eastern Pacific during the last 100 years. The reasons for their absence, however, remain to be determined.

Clearly, more investigation into the history of the distribution and harvesting of all age classes of bluefin tuna within the entire north Pacific will be necessary before we really understand the implications of the archeological remains reported in this study. Complex interactions of changes in ecological conditions and harvesting pressures on various age classes over the last 100 years probably have affected and may have had unexpected repercussions on the population structure of Pacific bluefin tuna. A better understanding of the distribution of adult tuna in the north Pacific through inclusion of archeological records may help document perturbations in the modern fishery.

Acknowledgments

The author would like to thank Richard Inglis, formerly of the Royal British Columbia Museum, Victoria, British Columbia, for his collection of ethnographic information and Bruce Collette at the Smithsonian Institution, Washington D.C., for confirmation of the taxonomic identity of the archeological material and for the loan of comparative specimens. Terry Foreman, a former associate of the Inter-American Tropical Tuna Commission, La Jolla, California, and Skip McKinnel, of the Department of Fisheries and Oceans Canada, Nanaimo, British Columbia, both supplied unbridled enthusiasm, encouragement and advice. The Royal British Columbia Museum in Victoria provided assistance in handling loaned material and photography. Greg Monks of the University of Manitoba, Winnipeg, helped enormously by setting aside tuna vertebrae as they were excavated from archeological deposits in Barkley Sound and allowed me immediate access to the material. This paper has been greatly improved through revision of earlier drafts by several anonymous reviewers; their efforts are much appreciated. Raw data are available on request from the author.

Literature cited

Bayliff, W. H.
1980. Synopsis of biological data on the northern bluefin tuna, *Thunnus thynnus* (Linnaeus, 1758), in the Pacific Ocean. Inter-Am. Trop. Tuna Comm., Spec. Rep. 2:262–293.
1993. Annual report of the Inter-American Tropical Tuna Commission, 1993, W. H. Bayliff (ed). IATTC, La Jolla, CA, 91 p.
1994. A review of the biology and fisheries for northern bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean. *In* R. S. Shomura, J. Majkowski, and S. Langi (eds.), Interactions of Pacific tuna fisheries, p. 244–295. FAO Fish. Tech. Paper 336(2).

Bayliff, W. H., Y. Ishizuka, and R. B. Deriso.
1991. Growth, movement, and attrition of northern bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean, as determined by tagging. Inter-American Tropical Tuna Comm. Bull. 20(1):1–94.

Bell, R. R.
1963. Synopsis of biological data on California bluefin tuna *Thunnus saliens* Jordan and Evermann 1926. FAO Fish. Rep. 6(2):380–421.

Calvert, S. G.
1980. A cultural analysis of faunal remains from three archaeological sites in Hesquiat Harbour, British Columbia. Ph.D. diss., Univ. British Columbia, Vancouver, 336 p.

Calvert, S. G., and S. J. Crockford.
1982. Appendix IV. *In* A. D. McMillan and D. E. St. Claire (eds.), Alberni prehistory: archaeological and ethnographic investigations on western Vancouver Island, p.174–219. Theytus Books, Penticton, British Columbia.

Cannon, A.
1991. The economic prehistory of Namu. Department of Archaeology Publ. 19, Simon Fraser Univ., Burnaby, British Columbia, 107 p.

Casteel, R. W.
1976. Fish remains in archaeology and palaeoenvironmental studies. Academic Press, San Francisco, CA, 180 p.

Crockford, S. J.
1994. New archaeological and ethnographic evidence of an extinct fishery for giant bluefin tuna (*Thunnus thynnus orientalis*) on the Pacific Northwest coast of North America. *In* W. Van Neer (ed.), Ann. Mus. R. Afri. Cent. Ser. Quarto Zool., p. 163–168. Sciences Zoologiques 274, Tervuren, Belgium.

Davis, S. J. M.
1987. The archaeology of animals. Yale Univ. Press, New Haven, CT, 224 p.

Dotson, R. C. and J. E. Graves.
1984. Biochemical identification of a bluefin establishes a new California size record. Calif. Fish Game 70(1):62–64.

Foreman, T. J. and Y. Ishizuka.
1990. Giant bluefin tuna off southern California, with a new California size record. Calif. Fish Game 76(3):181–186.
Hales, L. S., Jr., and E. J. Reitz.
1992. Historical changes in age and growth of Atlantic croaker, *Micropogonias undulatus* (Perciformes: Sciaenidae). J. Archaeol. Sci. 12:73–99.
Hart, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 p.
Holder, C. F.
1913. The game fishes of the world. Hodder and Stoughton, New York, NY.
Hubbs, C. L.
1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. J. Mar. Res. 7:459–482.
Huelsbeck, D. R.
1983. Mammals and fish in the subsistence economy of Ozette. Ph.D. diss., Washington State Univ., Pullman, WA, 166 p.
Kawasaki, T.
1991. Long-term variability in the pelagic fish populations. *In* T. Kawasaki, S. Tanaka, Y. Toba, and A. Taniguchi (eds), Long-term variability of pelagic fish populations and their environment, p. 47–60. Pergamon Press, Oxford.
Lamb, W. K. (ed.).
1984. A voyage of discovery to the North Pacific Ocean and round the world: 1791–1795, vol. II. The Hakluyt Soc., London, 437 p.
Leatherwood, S., R. R. Reeves, W. F. Perrin, and W. E. Evans.
1988. Whales, dolphins, and porpoises of the Eastern North Pacific and adjacent arctic waters: a guide to their identification. Dover Publications, Inc., New York, NY, 245 p.
Lyman, R. L.
1994. Vertebrate taphonomy. Cambridge Manuals in Archaeology, Cambridge Univ. Press.
Marshall, Y. M.
1993. A political history of the Nuu-Chah-nulth people: a case study of the Mowachaht and Muchalaht tribes. Ph.D. diss., Simon Fraser Univ., Burnaby, B.C., 467 p.
McMillan, A. D.
1979. Archaeological evidence for aboriginal tuna fishing on western Vancouver Island. Syesis 12:117–119.
Mitchell, D.
1988. Changing patterns of resource use in the prehistory of Queen Charlotte Strait, British Columbia. *In* B. L. Isaac (ed.), Research in economic anthropology, supplement 3: prehistoric economies of the Pacific Northwest coast, p. 245–290. JAI Press, Inc., Greenwich.
Mitchell, D., and L. Donald.
1988. Archaeology and the study of Northwest coast economies. *In* B. L. Isaac (ed). Research in economic anthropology, supplement 3: prehistoric economies of the Pacific Northwest coast, p. 293–351. JAI Press, Inc., Greenwich.
Moratto, M. J.
1984. California archaeology. Academic Press, San Francisco, CA, 756 p.
Nakamura, H.
1969. Tuna distribution and migration. Whitefriars Press, London, 76 p.
Neave, F.
1959. Records of fishes from waters of the British Columbian coast. J. Fish. Res. Board Can. 16(3):383–384.
Niimi, M.
1994. Sea mammal hunting in northern Japan during the Jomon period. Archeozoologia VI/2:37–56.
Otaishi, N.
1994. The Okhotsk culture: prehistoric hunting and fishing reconstructed from the Sea of Okhotsk paleofauna. Archaeozoologia VI/2:71–78.
Radovich, J.
1961. Relationships of some marine organisms of the northeast Pacific to water temperatures, particularly during 1957 through 1959. Calif. Fish Game, Fish. Bull. 112, 62 p.
Recksiek, C. W., and H. W. Frey.
1978. Biological, oceanographic, and acoustical aspects of the market squid (*Loligo opalescens* Berry). Calif. Fish Game, Fish. Bull. 169, 185 p.
Ringrose, T. J.
1993. Bone counts and statistics: a critique. J. Archaeol. Sci. 20:121–157.
Rivas, L. R.
1978. Preliminary models of annual life history cycles of the north Altantic bluefin tuna. *In* G. D. Sharp and A. E. Dizon (eds.), The physiological ecology of tunas, p. 369–393. Academic Press, New York, NY.
Rothschild, B. J.
1991. On the causes for variability of fish population—the linkage between large and small scales. *In* T. Kawasaki, S. Tanaka, Y. Toba, and A. Taniguchi (eds), Long-term variability of pelagic fish populations and their environment, p. 367–376. Pergamon Press, Oxford.
Sharp, G. D.
1978. Behavioral and physiological properties of tuna and their effects on vulnerability to fishing gear. *In* G. D. Sharp and A. E. Dizon (eds), The physiological ecology of tunas, p. 397–450. Academic Press, New York, NY.
Smith, P. J., A. M. Conroy, and P. R. Taylor.
1994. Biochemical-genetic identification of northern bluefin tuna *Thunnus thynnus* in the New Zealand fishery. N.Z. J. Mar. Freshwater Res. 28:113–118.
Wheeler, A., and A. K. G. Jones.
1989. Fishes. Cambridge Univ. Press, Cambridge, 210 p.

Dietary overlap of juvenile fall- and spring-run chinook salmon, *Oncorhynchus tshawytscha*, in Coos Bay, Oregon

Joseph P. Fisher
William G. Pearcy
College of Oceanic and Atmospheric Sciences
Oregon State University, Corvallis, Oregon 97331-5503
E-mail address: fisherjo@ucs.orst.edu

Abstract–During the summer of 1987 in Coos Bay, Oregon, dietary overlap (Schoener index) between juvenile fall-run chinook salmon, *Oncorhynchus tshawytscha*, and an introduced stock of juvenile hatchery-reared spring-run chinook salmon was high (0.82), indicating the potential for competition for food between these two groups in times of food scarcity. Both groups consumed a variety of prey, including fishes, adult insects, algae, barnacle molts, gammarid and caprellid amphipods, and juvenile decapods. Diets of both salmon groups varied with fish size and capture location. Overlap was low (0.25–0.55) between the smallest juvenile fall chinook salmon (≤80 mm FL), for which insects were the predominant prey (26% by weight), and all other length groups of both fall and spring chinook salmon, for which fish were the predominant prey (49%–94% by weight). Dietary overlap between both salmon groups was high in the lower bay (0.82), where fish prey predominated in the diets, and was also high in the mid bay (0.75), where algae and barnacle molts predominated in the diets. Three pieces of evidence suggest that the introduced hatchery-reared spring chinook salmon did not outcompete fall chinook salmon for food: 1) both the median stomach fullness and the percentage of stomachs containing food was higher for fall chinook salmon than for spring chinook salmon, 2) the median stomach fullness of fall chinook salmon was as high in the period following releases of spring chinook salmon into the bay as in the period prior to the releases, and 3) food of high caloric density (i.e. fish prey) formed an equally high proportion of the diets of both salmon groups, indicating that the quality of food eaten by both was similar.

Manuscript accepted 31 July 1996.
Fishery Bulletin 95:25–38 (1996).

Estuaries serve as rich feeding grounds and as refuges from predation for many juvenile subyearling fall-run (hereafter referred to as "fall") chinook salmon, *Oncorhynchus tshawytscha*, that reside in them for weeks or months before entering the ocean (Healey, 1980a, 1982, 1991; Myers, 1980; Kjelson et al., 1982; Myers and Horton, 1982; Simenstad et al., 1982). The survival of subyearling fall chinook salmon may be enhanced by extended residence in estuaries. Reimers (1973) reported that survival was greater among juvenile fall chinook salmon that resided in the Sixes River estuary from early summer through early fall than among those that quickly migrated through the estuary to the ocean in early summer.

Although there is much concern about the interaction between hatchery and wild stocks of salmon (Hilborn and Winton, 1993; Thomas and Mathisen, 1993; Winton and Hilborn, 1994), few reports document possible competition between groups of salmon for food in estuaries or the ocean. Peterman (1984) and Rogers and Ruggerone (1993) found negative correlations between size of sockeye salmon at different ages and their population and suggested that growth of sockeye salmon in the ocean was density dependent. Reimers (1973) and Neilson et al. (1985) found that the average growth rate of juvenile fall chinook salmon in the Sixes River estuary decreased during mid-summer when the population of juvenile salmon was high. Reimers (1973) attributed this drop in growth rate to intraspecific competition for limited food resources, leading to density-dependent growth, whereas Neilson et al. (1985), noting that the decrease in growth rate occurred during a period of increased abundance of the principal prey (*Corophium* sp.), suggested that lowered conversion efficiencies due to high temperatures in the estuary as well as intraspecific competition may have contributed to the drop in growth rate.

These studies suggest that releases of large numbers of hatchery salmon smolts into an estuarine basin could affect the native salmon in the system through competition for food in the estuary. The effect of competition on growth and survival of native fish would depend on several factors, among them the intensity and duration of the competition between the two groups. If the hatchery-reared fish eat different prey from that eaten by the wild fish, or if they move quickly through the estuary, their impact on the native fish may be relatively small. On the other hand, if the two groups

have similar feeding behaviors and if hatchery fish reside in the estuary for a substantial period, then the effect of hatchery fish on the wild fish may be great.

Anadromous, Inc. operated a salmon-rearing and release facility on the North Spit of Coos Bay, Oregon in the 1980's. From this facility millions of smolts are released into the bay annually, principally large subyearling spring-run ("spring") chinook salmon, thus creating the potential for competition between these hatchery-produced spring chinook salmon and the native runs of fall chinook salmon in the Coos Bay drainage.

During the late spring and summer of 1987 we undertook a sampling program in the lower half of Coos Bay to study the use of the estuary by different groups of juvenile chinook salmon. In 1987 two groups of juvenile chinook salmon were present in Coos Bay: fall chinook salmon from the Coos and Millacoma River drainages (both wild fish and fish released by the Salmon and Trout Enhancement Program [STEP]) and spring chinook salmon released from the saltwater rearing pens of the Anadromous, Inc. facility, North Spit of Coos Bay (Fig. 1). About 400,000 STEP fall chinook salmon were released in tributaries of the Coos River between 30 April and 28 June at average fork lengths (FL) of between 48 and 94 mm, and over five million spring chinook salmon (123–156 mm FL) were released from the Anadromous, Inc. release facility on North Spit between 19 June and 1 October. In an earlier paper (Fisher and Pearcy, 1990) we reported on the distributions and residence times of juvenile spring and fall chinook salmon in the bay. In this paper we describe the food habits of these two groups, overlap in their diets, and the potential for competition for food between them.

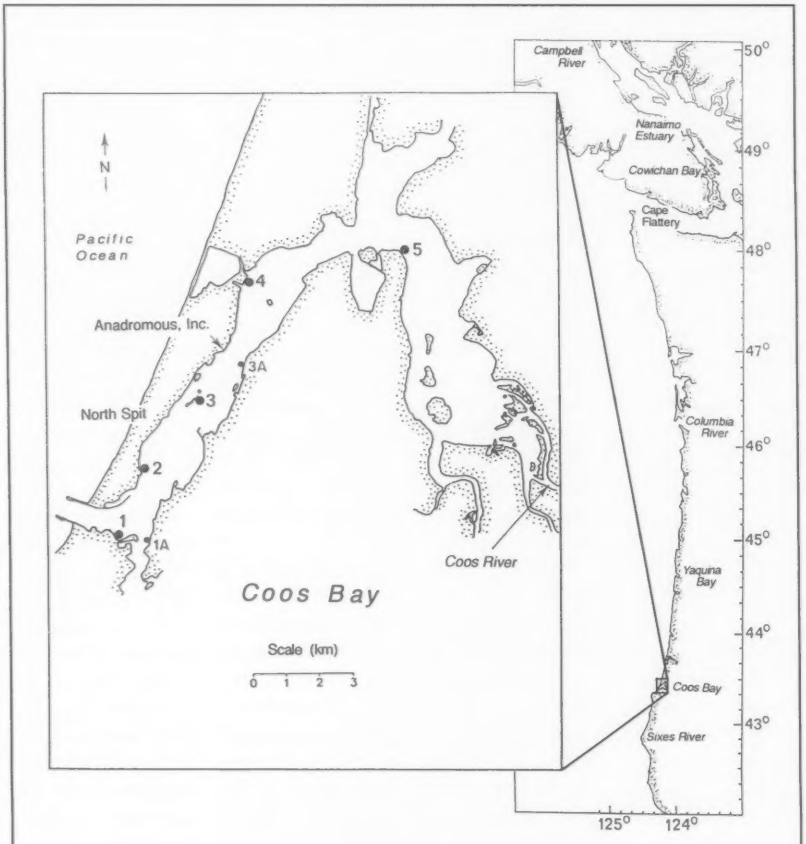


Figure 1

Map of Coos Bay, Oregon, showing the five stations sampled with beach seines in the summer of 1987. The lower bay and mid bays comprised stations 1–3 and 4–5 respectively.

Methods

Juvenile chinook salmon were caught by beach seine (60 m × 2.5 m with 19- and 13-mm mesh in the wings and bunt, respectively) at five locations on the margins of channels in the lower half of Coos Bay, Oregon, between late May and early October 1987 (Fig. 1). The substratum was sand at all but station 5, where it was a mixture of gravel fill and mud. At stations 2, 3, and 4, portions of eel grass beds were sampled during low tide. The area of Coos Bay we sampled was influenced strongly by the ocean and was highly marine in character with high salinities at all sampling sites, usually greater than 29 psu after mid-June. Water temperature (at 0.3 m depth) was fairly constant between May and October but increased with distance from the mouth, averaging 12.3°C at station 1 and 16.8°C at station 5 (Fisher and Pearcy, 1990).

Subsamples of juvenile chinook salmon caught in beach-seine sets were preserved in approximately 4% formaldehyde solution. Later, these were measured to the nearest mm FL and weighed to the nearest 0.01 g after excess moisture was removed by blotting. Stomachs were removed from 380 juvenile chinook salmon caught between 31 May and 4 September 1987 (Fig. 2). Stomach-content boluses were weighed to the nearest milligram after removing excess moisture by blotting. After weighing, they were preserved in 50% ethanol, then transferred to 75% ethanol.

At the time the stomach samples were obtained, the fish were examined for fin marks or for external parasites that could help to determine their origin. Most fish with clipped adipose fins also contained coded wire tags (CWT's) that identified them as spring chinook salmon produced at Anadromous, Inc. Fish with other fin clips were mainly STEP-reared fall chinook salmon released in freshwater tributaries of Coos Bay (Fisher and Pearcy, 1990).

The encysted metacercarial stage of a strigeoid trematode parasite is common in the skin of juvenile salmonids found in freshwater tributaries of Coos Bay. These cysts are surrounded by a black pigment that can be seen easily without magnification (Amandi[1]). The presence of metacercarial cysts on the skin or fins of juvenile chinook salmon caught in Coos Bay appeared to be a reliable indicator that the fish originated in the freshwater tributaries of the bay. Cysts were present on 43% of known fall chinook salmon (fin-marked STEP fish or fish caught before the first release of spring chinook salmon) and on 71% of small fish <101 mm FL (>2SD below the mean FL of most release groups of spring chinook salmon by Anadromous, Inc.). Conversely, cysts were absent on adipose-clipped spring chinook salmon and found on only 13% of fish in the size range of the spring chinook salmon released by Anadromous, Inc. (≥101 mm FL). Fish >100 mm FL with cysts were probably native salmon or STEP-reared fall chinook salmon that attained these greater lengths through growth. On the basis of this evidence, we classified fish caught in Coos Bay as fall chinook salmon if they met *any* of

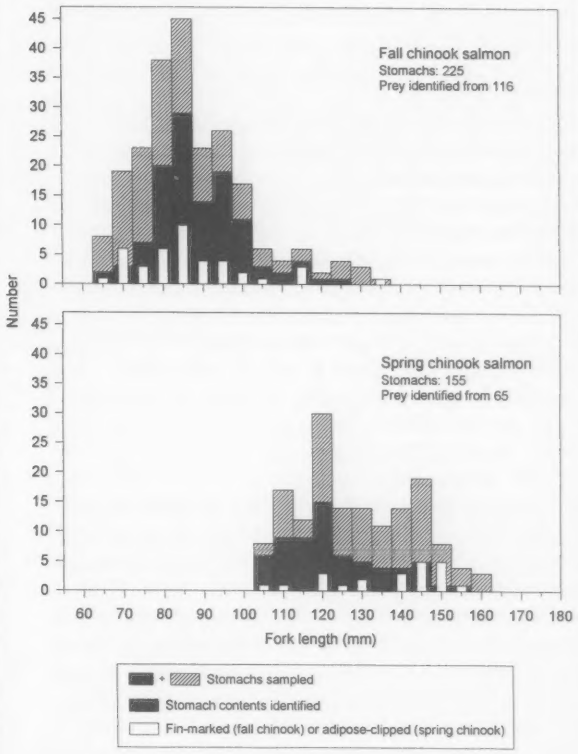


Figure 2

Length-frequency distributions of juvenile fish classified as fall and spring chinook salmon from which stomach samples were taken. Dark shading represents those stomach samples in which prey species were examined and identified. White bars in the upper and lower graphs represent numbers of fin-clipped STEP-reared fall chinook salmon and adipose clipped Anadromous, Inc.-reared spring chinook salmon, respectively.

[1] Amandi, T. 1995. Oregon Dep. Fish and Wildl., 516 Nash Hall, Oregon State Univ., Corvallis, OR 97331. Personal commun.

the following criteria: 1) they were caught before the first release of Anadromous, Inc. spring chinook salmon on 19 June; 2) metacercarial cysts were present on their skin or fins; 3) they had one of the STEP fin clips; or 4) they were ≤100 mm FL. Fish were classified as spring chinook salmon if they were ≥101 mm FL and did not meet any of the criteria for fall chinook salmon.

Stomach contents were examined and prey items identified to the lowest possible taxon from 116 fall chinook salmon and 65 spring chinook salmon collected between 29 June and 13 August 1987, the period of greatest overlap in the bay of the two groups (Fig. 2). Stomach contents from a single fall chinook salmon caught on 7 June were also examined.

Individual prey taxa in each stomach were weighed to the nearest 0.001 g after removing excess moisture by blotting. Those taxa that were too light to register on the scale (weight <0.0005 g), were assigned a weight of 0.0004 g. The estimated total weight of all food assigned this arbitrarily small value was only 0.05 g out of a total weight of 60.2 g for all taxa from all stomachs.

In the analyses of stomach contents, juvenile fall and spring chinook salmon were grouped by FL, by two collection areas ("lower bay," stations 1–3, and "mid-bay," stations 4–5) and by two sampling periods: 29 June to 17 July and 3–13 August. Within each class, the percent frequency of occurrence (FO) and percent by weight of each prey category in the diet was calculated. The percent by weight ($p_i \times 100$) of each prey category in each class was calculated as

$$100(p_i) = 100\left(\frac{\sum_{q=1}^{N} w_{iq}}{\sum_{q=1}^{N}\sum_{i=1}^{n} w_{iq}}\right), \quad (1)$$

where w_{iq} is the weight of food category i in fish q, n is the number of food categories, and N is the number of fish in the class.

Dietary overlap between classes was calculated by using the Schoener overlap index (ro; Schoener, 1970; Wallace, 1981; Linton et al., 1981):

$$ro = 1 - \frac{1}{2}\sum_{i=1}^{n}\left|p_{ij} - p_{ik}\right|, \quad (2)$$

where p_{ij} and p_{ik} are the proportions by weight of food category i (Eq. 1) in the diets of fish in classes j and k, respectively, and n is the number of food categories. Dietary overlap was calculated by using 14 categories of major prey and, because the overlap index is sensitive to the taxonomic resolution (Brodeur and Pearcy, 1992), it was also calculated by using the 86 lowest taxonomic levels identified (to genus or species in some cases). An overlap of ≥0.60 was considered significant (Zaret and Rand, 1971; Brodeur and Pearcy, 1992).

Results

Stomach fullness

The frequency distribution of stomach-content weight as a percentage of body weight ("stomach fullness") was skewed for both fall and spring chinook salmon (Fig. 3); therefore, nonparametric ranks tests were used to compare stomach fullness among different classes of fish. The median stomach fullness was higher for fall chinook salmon than for spring chinook salmon (2.4% vs. 1.2%, respectively; Mann Whitney (Wilcoxon) W test, W=11,630, P<0.0001). Stomachs were empty in a higher percentage of spring chinook salmon than of fall chinook salmon (16% vs. 1%), contributing to the difference in median stomach fullness of these two groups (Fig. 3).

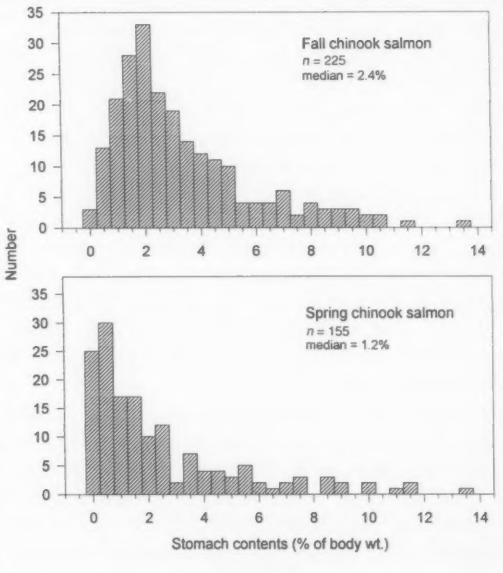


Figure 3

Frequency distributions of weight of stomach contents as a percentage of body weight for juvenile fall chinook salmon (top graph) and spring chinook salmon (bottom graph).

Range in stomach fullness was similar among fish of different lengths, and stomach contents weights of 8% of body weight or higher occurred in fish from 69 mm to 145 mm FL (Fig. 4). No significant difference in median stomach fullness was found among four FL classes (≤80 mm, 81–100 mm, 101–120 mm, and 121–140 mm) of fall chinook salmon (Kruskal-Wallace test, P=0.09). However, a significant difference in median stomach fullness was found among the three FL classes (101–120 mm, 121–140 mm, and ≥141 mm) of spring chinook salmon (Kruskal-Wallace test, P=0.03). Median stomach fullness was lowest (0.4%) for the largest spring chinook salmon (≥141 mm FL).

Median stomach fullness of fall chinook salmon was fairly constant during the study period, both before and after spring chinook salmon were released into the bay. No short-term decreases in stomach fullness of fall chinook salmon were associated with individual releases of spring chinook salmon, except for the 4 August release (Fig. 5). Conversely, median stomach fullness of spring chinook salmon was low immediately following releases of large numbers of spring chinook salmon from the Anadromous, Inc. facility, especially the 4 August and the August 31–3 September releases (Fig 5).

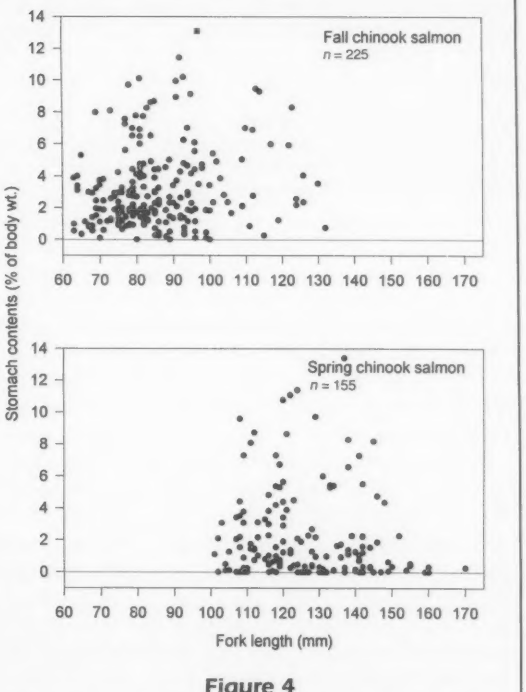


Figure 4

Weight of stomach contents as a percentage of body weight versus fish length for juvenile fall chinook salmon (top graph) and spring chinook salmon (bottom graph).

Diets of fall and spring chinook salmon

Percent FO and percent by weight of fourteen major prey categories from stomachs of juvenile fall and spring chinook salmon are summarized in Table 1. By weight, juvenile or larval fish were dominant prey of both fall and spring chinook salmon, representing 64% and 65% of the total weight of stomach contents, respectively. The fish prey of fall chinook salmon were juvenile smelt, unidentified fish remains, *Ammodytes hexapterus*, juvenile *Sebastes* sp., and an unidentified cottid, representing 41%, 10%, 8%, 6%, and <1% of stomach-content weight, respectively. Fish prey of spring chinook salmon were similar: juvenile smelt, *Ammodytes hexapterus*, unidentified fish remains, and *Sebastes sp.*, accounted for 49%, 13%, 3%, and <1% of stomach-content weight, respectively.

Other prey categories accounted for much smaller fractions of stomach-content weights of the two groups of juvenile chinook salmon. Of the nonfish prey, insects and plants (mainly algae) composed the largest fractions by weight in stomachs of fall chinook salmon (8% and 7%, respectively), whereas plants (mainly the algae *Ulva* sp. and *Enteromorpha* sp.) and barnacle molts composed the largest fractions by weight in stomachs of spring chinook salmon (16% and 12%, respectively; Table 1).

The most numerous insects[2] in fall chinook salmon stomachs were adults of terrestrial taxa (61% of the total) and adults of taxa having aquatic or semi-aquatic larvae (36% of the total). Larvae and pupae composed only 3% of the total number of individuals. Adults in the orders Diptera, Hemiptera, Homoptera, Pscoptera, Hymenoptera, Coleoptera, and Trichoptera accounted for 33%, 23%, 15%, 10%, 7%, 6%, and 2% of the total number of insects in fall chinook salmon stomachs, respectively. The most numerous taxa in these insect orders (and their percentages of total insect numbers) were midges (Chironomidae; 25%), plant bugs (Miridae; 22%), aphids (Aphididae; 11%), book and bark lice (10%), parisitoid wasps (5%), rove beetles (Staphylinidae; 4%), and caddis flies (2%), respectively.

Although insects were a much larger fraction by weight of the diet of fall chinook salmon than of the diet of spring chinook salmon (8% vs. 1%, respectively, Table 1), they occurred frequently in stomachs of both salmon groups (80% and 60%, respectively). Many of the same insect taxa were consumed by both fall

[2] The different insect taxa were not weighed separately, but individuals of each taxon were counted.

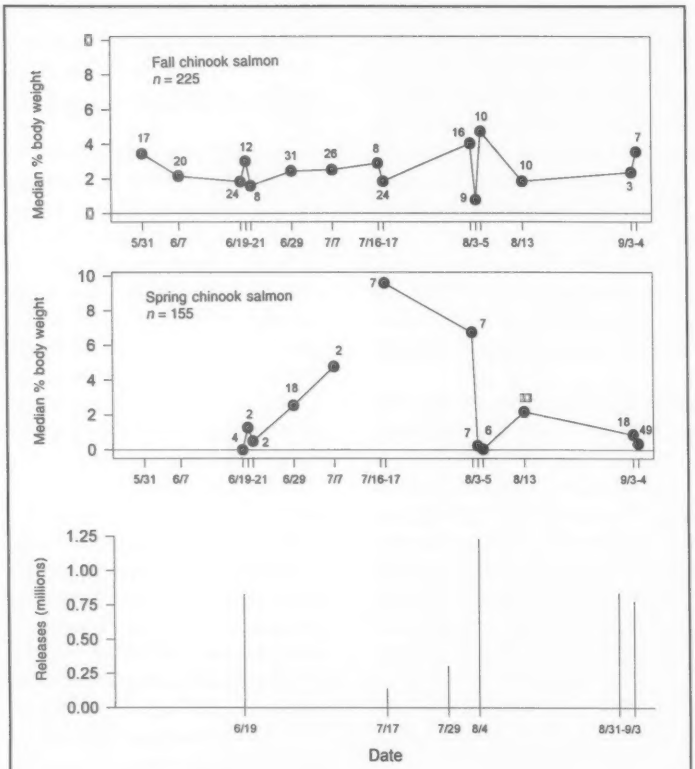

Fall chinook salmon
n = 225
Median % body weight
5/31 6/7 6/19-21 6/29 7/7 7/16-17 8/3-5 8/13 9/3-4
Spring chinook salmon
n = 155
Median % body weight
5/31 6/7 6/19-21 6/29 7/7 7/16-17 8/3-5 8/13 9/3-4
Releases (millions)
6/19 7/17 7/29 8/4 8/31-9/3
Date

Figure 5

Median weight of stomach contents as a percentage of body weight by sampling date for fall chinook salmon (top graph) and spring chinook salmon (middle graph). Numbers indicate sample size. Numbers of spring chinook salmon released into Coos Bay by Anadromous, Inc. on different dates are also shown (bottom graph).

and spring chinook salmon. The most numerous insects from spring chinook salmon stomachs were chironomids (31%), book and bark lice (23%), aphids (9%), tipulids (crane flies, 8%), and plant bugs (4%).

Other prey categories that occurred frequently in stomachs of both fall and spring chinook salmon were barnacle molts (47% and 51%, respectively), algae and other plant material (46% and 68%), gammarid amphipods (41% and 43%), fishes (40% and 37%), and crab larvae (27% and 35%). Isopods, caprellid amphipods, nonanomuran or nonbrachyuran decapod larvae, spiders, unidentified arthropods, and molluscs were less common, occurring in 14% or fewer of stomachs

Gammarid amphipods were a moderately important component of the diet of fall chinook salmon (4% by weight), but were less important in the diet of spring chinook salmon (only 1% by weight). A variety of gammarid species were eaten by fall chinook salmon, the most abundant were *Jassa* spp. unidentified gammarids, *Megalorchestia pugettensis*, *Ischyrocerus* spp., *Atylus tridens*, and *Corophium* spp. (2.0%, 0.6%, 0.3%, 0.2%, 0.2%, and 0.1% of total food weight respectively).

Dietary overlap between juvenile fall and spring chinook salmon, according to the relative weights (Eq. 2) of the 14 major food categories (Table 1), was high (0.82), owing largely to the predominance of fish prey in diets of both groups. Diet overlap based on relative weights of prey identified to the lowest possible taxonomic level (86 categories of varying taxonomic level) was lower but still relatively high (0.66).

Diets by fish length

Insect prey were relatively more important and fish prey were relatively less important in the diet of the

Table 1

Percentage by weight and frequency of occurence (in parentheses) of fourteen major food categories in stomachs of juvenile fall-run and spring-run chinook salmon caught in 1987 in Coos Bay. Numbers in brackets are sample sizes.

Food category	Fall chinook salmon [116]	Spring chinook salmon [65]
Cirripedia molts	5 (47)	12 (51)
Isopods	<1 (9)	<1 (11)
Caprellid amphipods	1 (14)	<1 (11)
Gammarid amphipods	4 (41)	1 (43)
Brachyuran, anomuran larvae	2 (27)	2 (35)
Other decapod larvae	<1 (8)	<1 (2)
Crustacean fragments	5 (20)	1 (25)
Araneae	<1 (14)	<1 (5)
Insects	8 (80)	1 (60)
Other arthropods	<1 (6)	<1 (2)
Molluscs	<1 (4)	<1 (12)
Teleosts	64 (40)	65 (37)
Algae, plants	7 (46)	16 (68)
Other material	4 (43)	2 (55)

Table 2

Percentage by weight and frequency of occurence (in parentheses) of fourteen major food categories in stomachs of different size groups of fall and spring chinook salmon caught in 1987 in Coos Bay. Numbers in brackets are sample sizes.

	Fall chinook salmon FL (mm)			Spring chinook salmon FL (mm)		
Food category	≤80 [32]	81–100 [73]	≥101 [11]	101–120 [39]	121–140 [19]	≥141 [7]
Cirripedia molts	9 (63)	5 (45)	3 (18)	22 (62)	9 (42)	<1 (14)
Isopods	<1 (9)	<1 (10)	0	<1 (10)	<1 (16)	0
Caprellid amphipods	1 (9)	1 (18)	0	<1 (8)	<1 (16)	<1 (14)
Gammarid amphipods	4 (44)	5 (42)	<1 (18)	1 (51)	1 (37)	<1 (14)
Brachyuran, anomuran larvae	7 (25)	2 (32)	0	1 (28)	2 (42)	3 (57)
Other decapod larvae	<1 (13)	<1 (7)	0	0	<1 (5)	0
Crustacean fragments	11 (22)	6 (22)	0	2 (23)	1 (32)	<1 (14)
Araneae	<1 (13)	<1 (16)	0	<1 (5)	<1 (5)	0
Insects	26 (94)	7 (81)	1 (36)	1 (69)	<1 (63)	0
Other arthropods	<1 (13)	<1 (4)	0	0	<1 (5)	0
Molluscs	1 (6)	<1 (4)	0	<1 (5)	<1 (26)	<1 (14)
Teleosts	18 (9)	62 (45)	94 (91)	49 (31)	68 (32)	91 (86)
Algae, plants	12 (56)	7 (42)	2 (36)	20 (72)	18 (63)	4 (57)
Other material	11 (59)	4 (38)	<1 (27)	4 (59)	<1 (42)	2 (71)

smallest fall chinook salmon (≤80 mm FL) than in the diets of the other length groups of both fall and spring chinook salmon. Insect prey made up 26% of food by weight in stomachs of the smallest fall chinook salmon (Table 2). The insect fraction of the diet dropped to 7% and 1% for larger fall chinook salmon 81–100 mm FL and ≥101 mm FL, respectively, and was ≤1% for all length groups of spring chinook salmon. Fish made up only 18% by weight of the diet of fall chinook salmon ≤80 mm FL, but 62% and 94% by weight of the diet of fall chinook salmon 81–100 mm FL and ≥101 mm FL, respec-

tively, and between 49% and 91% by weight of the diet of spring chinook salmon.

Larval crab (anomuran and brachyuran) prey were a moderately important component of the diet of the two smallest length classes of fall chinook salmon (≤80 mm FL and 81–100 mm FL) and of the two largest length classes of spring chinook salmon (121–141 mm FL and ≥141 mm FL), representing 7% and 2%, and 2% and 3% of total food by weight, respectively (Table 2). However, crab larvae of various taxa and at different developmental stages were consumed by chinook salmon of different stock and length groups. The smallest fall chinook salmon (≤80 mm FL) fed mainly on porcellanid, pinnotherid, callianassid, and unidentified brachyuran zoea rather than on megalopae (95% zoea and 5% megalopae by weight), whereas larger fall chinook salmon (81–100 mm FL) fed more on megalopae than on zoea (69% vs. 31% by weight), and the large spring chinook salmon (≥121 mm FL) fed exclusively on megalopae, mainly large *Cancer magister* (72%), *Cancer oregonensis* (19%), and *Cancer* sp. (4%).

Gammarid amphipods were also a fairly important component of the diet of the small fall chinook salmon, representing 4% and 5% by weight for fish ≤80 mm FL and 81–100 mm FL, respectively, but were a less important component of the diets of the largest fall chinook salmon (≥101 mm FL) and spring chinook salmon (Table 2).

Dietary overlap, based on the 14 major prey categories was low (≤0.55) between the smallest fall chinook salmon (≤80 mm FL) and all other length categories of fall and spring chinook salmon (Table 3). This reflects the reduced relative importance of fish and the greater relative importance of insects and crab larvae in the diet of the smallest fall chinook salmon than in the diet of larger fish (Table 2). Excluding the smallest fall chinook salmon, diet overlap was high for eight of ten comparisons among length groups of fall and spring chinook salmon (Table 3).

Dietary overlap, in respect to the lowest identified taxa (86 categories) was also low between fall chinook salmon ≤80 mm FL and all other groups. Overlap among the other groups was generally higher than that with the small fall chinook salmon but was ≥0.60 for only four of the ten comparisons.

Diets by location

Dramatic differences in the diets of fall and spring chinook salmon were associated with where the fishes were caught in the bay. For both salmon groups, fish were a much more important component of the diet at lower-bay stations 1–3 than at mid-bay stations 4–5 (Table 4). Conversely, barnacle molts and algae made up a much larger fraction of stomach contents at mid-bay stations than at lower-bay stations (Table 4). Dietary overlap based on the 14 major food categories was high between fall and spring chinook salmon caught in the same areas of the bay but was low for all comparisons of salmon caught in the two different areas of the bay (Table 5). Dietary overlap based on the 86 lower taxonomic categories was also highest for fall and spring chinook salmon caught in the same area of the bay, but only for fish caught in the lower bay was the overlap value ≥0.60 (Table 5).

Table 3

Dietary overlap of different length groups of fall and spring chinook salmon. Overlap values based on 14 major food categories are in normal type and those based on 86 lower taxonomic categories are in italics. High overlap values (≥0.60) are in bold type.

		Fall chinook salmon FL (mm)		Spring chinook salmon FL (mm)		
		81–100	≥101	101–120	121–140	≥141
Fall chinook salmon FL (mm)	≤80	0.55	0.25	0.48	0.44	0.27
		0.36	*0.13*	*0.25*	*0.21*	*0.07*
	81–100	—	**0.68**	**0.70**	**0.79**	**0.70**
			0.56	*0.57*	***0.67***	*0.46*
	≥101	—	—	0.55	***0.74***	**0.94**
				0.35	***0.63***	***0.72***
Spring chinook salmon FL (mm)	101–120	—	—	—	**0.80**	0.56
					0.63	*0.32*
	121–140	—	—	—	—	**0.74**
						0.59

Diets by sampling period

Between two sampling periods (29 June–17 July and 3–13 August) moderate changes occurred in the proportions of the 14 major food categories in stomachs of both fall and spring chinook salmon. In stomachs of fall chinook salmon, the percentage by weight of insects, gammarid amphipods, and crab larvae was higher in the earlier than in the later period, whereas the percentage by weight of fish prey was higher in the later than in the earlier period (Table 6). In spring chinook salmon stomachs, barnacle molts and fish were more abundant in the earlier period than in the later period, whereas algae and crab larvae were more abundant in the later period than in the earlier period.

Despite these shifts in prey composition, diet overlap based on the 14 major prey categories was high for all comparisons of fall and spring chinook salmon caught in the two time periods (Table 7). However,

Table 4

Percentage by weight and frequency of occurrence (in parentheses) of fourteen major food categories in stomachs of fall and spring chinook salmon caught in 1987 in the lower (stations 1–3) and mid (stations 4–5) sections of Coos Bay. Numbers in brackets are sample sizes. Mean fork lengths (FL) of fish in each area are also shown.

	Fall chinook salmon		Spring chinook salmon	
Food category	Sta. 1–3 87 mm FL [90]	Sta. 4–5 88 mm FL [26]	Sta. 1–3 123 mm FL [39]	Sta. 4–5 118 mm FL [26]
Cirripedia molts	2 (39)	22 (77)	4 (33)	35 (77)
Isopods	<1 (4)	<1 (23)	<1 (8)	<1 (15)
Caprellid amphipods	1 (14)	1 (12)	<1 (15)	<1 (4)
Gammarid amphipods	4 (42)	2 (35)	<1 (33)	2 (58)
Brachyuran, anomuran larvae	2 (28)	6 (23)	2 (44)	1 (23)
Other decapod larvae	<1 (10)	0	<1 (3)	0
Crustacean fragments	6 (22)	3 (12)	1 (26)	1 (23)
Araneae	<1 (12)	<1 (19)	<1 (3)	<1 (8)
Insects	6 (76)	17 (96)	<1 (49)	1 (77)
Other arthropods	<1 (6)	1 (8)	0	<1 (4)
Molluscs	<1 (2)	1 (12)	<1 (13)	<1 (12)
Teleosts	71 (47)	14 (15)	79 (54)	24 (12)
Algae, plants	3 (37)	31 (77)	11 (56)	32 (84)
Other material	4 (44)	3 (38)	1 (54)	3 (58)

Table 5

Dietary overlap of fall and spring chinook salmon caught in the lower (stations 1–3) and mid (stations 4–5) sections of Coos Bay. Overlap values based on 14 major food categories are in normal type and those based on 86 lower taxonomic categories are in italics. High overlap values (≥0.60) are in bold type.

		Fall chinook salmon	Spring chinook salmon	
		Sta. 4–5	Sta. 1–3	Sta. 4–5
Fall chinook salmon	Sta. 1–3	0.37 *0.28*	**0.82** ***0.68***	0.38 *0.35*
	Sta. 4–5	—	0.35 *0.22*	**0.75** *0.47*
Spring chinook salmon	Sta. 1–3	—	—	0.43 *0.41*

Table 6

Percentage by weight and frequency of occurrence (in parentheses) of fourteen major food categories in stomach of juvenile fall and spring chinook salmon caught during two time periods in 1987 in Coos Bay. Numbers in brackets are sample sizes. Mean fork lengths (FL) of fish caught during each time are also shown.

	Fall chinook salmon		Spring chinook salmon	
Food category	29 Jun–17 Jul 85 mm FL [89]	3–13 Aug 95 mm FL [26]	29 Jun–17 Jul 117 mm FL [26]	3–13 Aug 123 mm FL [39]
Cirripedia molts	6 (54)	3 (23)	17 (65)	8 (41)
Isopods	<1 (11)	0	<1 (4)	<1 (15)
Caprellid amphipods	1 (17)	<1 (4)	<1 (12)	<1 (10)
Gammarid amphipods	6 (47)	<1 (19)	1 (38)	1 (46)
Brachyuran, anomuran larvae	2 (29)	<1 (15)	1 (27)	2 (41)
Other decapod larvae	<1 (10)	0	0	<1 (3)
Crustacean fragments	9 (24)	<1 (8)	<1 (15)	2 (31)
Araneae	<1 (17)	<1 (4)	<1 (8)	<1 (3)
Insects	11 (84)	2 (65)	<1 (65)	1 (56)
Other arthropods	<1 (8)	0	<1 (4)	0
Molluscs	<1 (3)	<1 (8)	0	<1 (21)
Teleosts	51 (36)	84 (54)	73 (38)	58 (36)
Algae, plants	6 (45)	7 (50)	6 (62)	24 (72)
Other material	5 (47)	3 (31)	1 (38)	3 (67)

diet overlap based on the lowest identified taxa (86 categories) was low for all comparisons except that between fall and spring chinook salmon caught in the period 3–13 August. Although a variety of fish prey were eaten by both salmon groups during the earlier period, during the later period fish prey were nearly all juvenile osmerids.

Discussion

Potential for competition

The high dietary overlap values (Tables 3, 5, 7) between juvenile fall chinook salmon ≥81 mm FL and hatchery spring chinook salmon suggest that there is the potential for competition for food between these two groups in Coos Bay under conditions of food limitation. However, whether or not the two groups were competing for food in 1987 cannot be determined from dietary overlap alone. In fact, high dietary overlap may sometimes indicate a condition in which abundant food resources are shared between potential competitors rather than a condition in which there is competition for a resource in short supply (Zaret and Rand, 1971; Myers, 1980). Zaret and Rand (1971), in a study of tropical stream fishes, found that dietary overlap between species was high during the rainy season, when food resources were abundant, and low during the dry season, when food resources were scarce and when the different fish species targeted different prey.

We found little evidence in this study that the introduced hatchery-reared spring chinook salmon outcompeted native and STEP-reared fall chinook salmon for food. One potential result of competition for food between groups is a shift to less desirable prey in the diet of the weaker competitors (Hanson and Leggett, 1986). However, during the period when both fall and spring chinook salmon were in Coos Bay, calorically dense (high-quality) fish prey made up an equally large fraction by weight of the diets of both salmon groups (Table 1); i.e. fall chinook salmon were eating just as nutritious prey as that eaten by spring chinook salmon. Another potential result of competition is a decrease in growth rate (or average stomach fullness) of one or all of the competing groups (Reimers, 1973; Nielson et al., 1985; Hanson and Leggett, 1986). If spring chinook salmon outcompeted fall chinook salmon for food, the average stomach fullness of fall chinook salmon might be expected to drop following releases of the spring chinook salmon; this, however, did not occur. Stomach fullness of fall chinook salmon was equally high in the periods be-

Table 7

Dietary overlap of fall and spring chinook salmon during two time periods. Overlap values based on 14 major food categories are in normal type and those based on 86 lower taxonomic categories are in italics. High overlap values (≥0.60) are in bold type.

		Fall chinook salmon	Spring chinook salmon	
		3–13 Aug	29 Jun–17 Jul	3–13 Aug
Fall chinook salmon	29 Jun–17 Jul	**0.66**	**0.67**	**0.73**
		0.26	*0.44*	*0.32*
	3–13 Aug	—	**0.83**	**0.73**
			0.49	***0.70***
Spring chinook salmon	29 Jun–17 Jul	—	—	**0.75**
				0.56

fore and after spring chinook salmon were released into the bay (Fig. 5). In fact, stomach fullness of fall chinook salmon was usually higher than that of spring chinook salmon throughout the study period (Figs. 3 and 5). The low stomach fullness among spring chinook salmon following releases from the Anadromous, Inc. facility (Fig. 5) may reflect a delay in the start of feeding on natural prey by these hatchery fish. Paszkowski and Olla (1985) suggested that the inability of some hatchery fish to adapt to the natural environment may contribute to the poor survival of some groups of hatchery salmon. We conclude that the high dietary overlap between juvenile fall and spring chinook salmon indicates the potential for competition for food between these salmon groups in Coos Bay, but that in the summer of 1987 there was little evidence of actual food limitation or competition.

Differences between smaller fall chinook salmon and larger hatchery spring chinook salmon in spatial distribution and duration of residence within estuaries may tend to minimize their competition for food. Small fish tend to occur in shallow, nearshore areas or in salt marshes, whereas large fish tend to occur in deeper channel areas (Healey, 1980a, 1991; Kjelson et al., 1982; Levings, 1982; Simenstad et al., 1982; McCabe et al., 1986; Macdonald et al., 1987). Larger juvenile chinook salmon also tend to spend less time in estuaries than do smaller fish (Myers, 1980; Simenstad and Wissmar, 1984; Fisher and Pearcy, 1990). Both these differences may tend to decrease competition for food between hatchery-reared and wild chinook salmon in estuaries if there is a large difference in their size. However, large releases of hatchery salmon smolts into an estuary may affect wild smolts detrimentally by attracting birds and other predators that prey on juvenile salmon (Emlen et al., 1990).

We did not investigate rates of secondary production in the bay, rates of exchange of prey between the adjacent ocean and the bay, the rations required by juvenile salmon to maintain optimum growth rates, or the fractions of available prey in the bay eaten by juvenile salmon and other potential competing species. Without such information it is difficult to assess the likelihood that the growth and survival of juvenile salmon was limited by food in Coos Bay in 1987. The lower half of Coos Bay is strongly influenced by the adjacent ocean (Burt and McAlister, 1959; Fisher and Pearcy, 1990). In a study of Yaquina Bay, an Oregon estuary with physical characteristics similar to Coos Bay, Myers (1980) suggested that much of the food for juvenile salmon residing in the bay was supplied by tidal exchange with the ocean. Undoubtedly, the productivity of the adjacent ocean has a strong influence on the capacity of Coos Bay to support juvenile chinook salmon.

Upper-bay and lower-bay gradients in diet

Between the mid and lower sections of Coos Bay the diet of juvenile fall chinook salmon shifted from predominantly drift insects, barnacle molts, and drift algae to predominantly marine fishes (Table 4). A similar increase in piscivory in the lower bay also occurred among spring chinook salmon (Table 4).

Shifts in the diet of juvenile chinook salmon as they move from the river, through the estuary, and to the ocean appear to be related to the changes in habitat and foraging behavior which occur as a consequence of growth and development. Macdonald et al. (1987) observed that large hatchery-reared chinook salmon were often found in deeper, more saline waters of the salt-wedge of the Campbell River estuary, whereas smaller wild chinook salmon were often found in the freshwater layer near the surface. Small

fry and subyearling chinook salmon often use tidal marshes where they eat drift and emergent insects and epibenthic crustaceans (Kjelson et al., 1982; Simenstad et al., 1982; Levings et al., 1991; Shreffler et al., 1992), whereas, larger, yearling chinook salmon spend little time in salt marshes but quickly move to neritic habitats (Simenstad et al., 1982). When subyearling fish move to neritic habitats their diet shifts to fishes, decapod larvae, euphausiids, and drift insects (Simenstad et al., 1982). McCabe et al. (1986) observed that, in the Columbia River estuary, subyearling chinook salmon in pelagic areas were significantly larger than those caught in shallow intertidal habitats and that the prey of juvenile chinook salmon varied with season, habitat, and position in the estuary. Feeding behavior is also influenced by environmental factors, for example turbidity (Gregory and Northcote, 1993).

Diets of juvenile chinook salmon in freshwater reaches of river systems often are dominated by larval, pupal, or adult insects that are captured mainly in the drift at the surface or in the water column (Becker, 1973; Craddock et al., 1976; Sagar and Glova, 1987, 1988; Rondorf et al., 1990; Healey, 1991; Levings and Lauzier, 1991; Smirnov et al., 1994). Depending on season and habitat, both terrestrial insects as well as different developmental stages of aquatic insects can be important prey for chinook salmon in rivers (Rondorf et al., 1990; Levings and Lauzier, 1991). Insects are also important constituents of the diets of juvenile chinook salmon in many estuaries (Healey, 1980, a and b, 1982, 1991; Levings, 1982; McCabe et al., 1986; Kask et al., 1988; this study), particularly in fresh or brackish water tidal marshes (Kjelson et al., 1982; Levings et al., 1991; Shreffler et al., 1992).

Whereas insects are important prey in freshwater and upper estuaries, fishes are important prey of juvenile chinook salmon constituents in the lower reaches of estuaries as well as in marine, neritic or subtidal areas (Healey, 1980a; Myers, 1980; Kjelson et al., 1982; Simenstad et al., 1982; Argue et al., 1986; McCabe et al., 1986; Levings et al., 1991; Reimers et al.[3]; Nicholas and Lorz[4]). Fish prey are also predominant in the diets of juvenile chinook salmon in marine waters off Oregon and Washington (Peterson et al., 1982; Emmett et al., 1986; Brodeur and Pearcy, 1990, 1992; Brodeur et al., 1992), in the Gulf Islands area of the Strait of Georgia (Healey, 1980b), and in the Fraser River plume (St. John et al., 1992).

In Coos Bay, the increase in importance of marine fish in the diets of juvenile fall and spring chinook salmon at the lower-bay stations may reflect an upper-bay, lower-bay gradient in the abundance of fish prey. Juvenile osmerids, sandlance, and rockfish were the predominant fish prey of juvenile chinook salmon in Coos Bay. In Yaquina Bay, larval and juvenile stages of these species were present in peak abundances in plankton samples from the extreme lower-bay and offshore stations (Pearcy and Myers, 1974). Myers (1980) caught more species of fishes in the lower than in the upper section of Yaquina Bay and suggested that much of the food for juvenile chinook salmon residing in the bay was supplied by tidal exchange with the ocean. She also suggested that high temperatures in the upper bay inhibited movement of predominantly marine species into the upper bay. A similar mechanism may be operating in Coos Bay. In our beach-seine samples large juvenile and adult surf smelt were much more abundant at lower than at mid-bay stations (average catch per set was 2,290, 237, 108, 30, and 12 at stations 1, 2, 3, 4, and 5, respectively). If, as was the case in Yaquina Bay, smaller larval and juvenile smelt also are more abundant in lower Coos Bay, the increased consumption by juvenile chinook salmon of these fish prey in the lower bay may be a consequence of their greater density there.

Acknowledgments

We thank John Chapman for assistance in the identification of gammarid amphipods. Jim Digiulio of Aquatic Biology Associates identified the insect prey. Carl Brookins, Alton Chung, Matt Wilson, Ann Raich, and Karen Young assisted in the field, and Terrin Ricehill assisted in the laboratory; their help is greatly appreciated. Three anonymous reviewers provided very helpful comments on earlier drafts of this manuscript. This study was supported by NOAA, Northwest Fisheries Science Center, Grant NA47FE0182-02.

Literature cited

Argue, A. W., B. Hillaby, and C. D. Shepard.
1936. Distribution, timing, change in size, and stomach contents of juvenile chinook and coho salmon caught in Cowichan Estuary and Bay, 1973, 1975, 1976. Can. Tech. Rep. Fish. Aquat. Sci. 1431, 168 p.

[3] Reimers, P. E., J. W. Nicholas, T. W. Downey, R. E. Halliburton, and J. D. Rogers. 1978. Fall chinook ecology project, AFC-76-2. Federal Aid Progress Reports, Fisheries. Oregon Dep. Fish and Wildl., 2501 S.W. First Ave., P.O. Box 59, Portland, OR 97207.

[4] Nicholas, J. W., and H. V. Lorz. 1984. Stomach contents of juvenile wild chinook and juvenile hatchery coho salmon in several Oregon estuaries. Oregon Dep. Fish and Wildl., 2501 S.W. First Ave., P.O. Box 59, Portland, OR 97207. Progress Rep. 84-2, 9 p.

Becker, C. D.
1973. Food and growth parameters of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in central Columbia River. Fish. Bull. 71:387–400.

Brodeur, R. D., R. C. Francis, and W. G. Pearcy.
1992. Food consumption of juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tschawytscha*) on the continental shelf off Washington and Oregon. Can. J. Fish. Aquat. Sci. 49:1670–1685.

Brodeur, R. D., and W. G. Pearcy.
1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington Coast. Fish. Bull. 88:617–636.
1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. Mar. Ecol. Prog. Ser. 84:101–119.

Burt, W. V., and W. B. McAlister.
1959. Recent studies in the hydrography of Oregon estuaries. Oreg. Fish Comm. Res. Briefs 7(1):14–27.

Craddock, D. R., T. H. Blahm, and W. D. Parente.
1976. Occurrence and utilization of zooplankton by juvenile chinook salmon in the lower Columbia River. Trans. Am. Fish. Soc. 105:72–76.

Emlen, J. M., R. R. Reisenbichler, A. M. McGie, and T. E. Nickelson.
1990. Density-dependence at sea for coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 47:1765–1772.

Emmett, R. L., D. R. Miller, and T. H. Blahm.
1986. Food of juvenile chinook, *Oncorhynchus tshawytscha*, and coho, *O. kisutch*, salmon off the northern Oregon and southern Washington coasts, May–September 1980. Calif. Fish Game 72(1):38–46.

Fisher, J. P., and W. G. Pearcy.
1990. Distribution and residence times of juvenile fall and spring chinook salmon in Coos Bay, Oregon. Fish. Bull. 88:51–58.

Gregory, R. S., and T. G. Northcote.
1993. Surface, planktonic and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can. J. Fish. Aquat. Sci. 50:233–240.

Hanson, J. M., and W. C. Leggett.
1986. Effect of competition between two freshwater fishes on prey consumption and abundance. Can. J. Fish. Aquat. Sci. 43:1363–1372.

Healey, M. C.
1980a. Utilization of the Nanaimo River estuary by juvenile chinook salmon, *Oncorhynchus tshawytscha*. Fish. Bull. 77:653–668.
1980b. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* W. J. McNeil and D. C. Himsworth (eds.), Salmonid ecosystems of the North Pacific, p. 203–229. Oregon State Univ. Press, Corvallis, OR.
1982. Juvenile Pacific salmon in estuaries: the life support system. *In* V. S. Kennedy (ed.), Estuarine comparisons, p. 315–341. Academic Press, New York, NY.
1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). *In* C. Groot and L. Margolis (eds.), Pacific salmon life histories, p. 313–393. Univ. British Columbia Press, Vancouver.

Hiborn, R., and J. Winton.
1993. Learning to enhance salmon production: lessons from the Salmonid Enhancement Program. Can. J. Fish. Aquat. Sci. 50:2043–2056.

Kask, B. A., T. J. Brown, and C. D. McAllister.
1988. Neashore epibenthos of the Campbell River estuary and Discovery Passage, 1983, in relation to juvenile chinook diets. Can. Tech. Rep. Fish. Aquat. Sci. 1616, 71 p.

Kjelson, M. A., P. F. Raquel, and F. W. Fisher.
1982. Life history of fall-run juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento–San Joaquin estuary, California. *In* V. S. Kennedy (ed.), Estuarine comparisons, p. 393–411. Academic Press, New York, NY.

Levings, C. D.
1982. Short term use of a low tide refuge in a sandflat by juvenile chinook, (*Oncorhynchus tshawytscha*), Fraser River estuary. Can. Tech. Rep. Fish. Aquat. Sci. 1111, 33 p.

Levings, C. D., K. Conlin, and B. Raymond.
1991. Intertidal habitats used by juvenile chinook salmon (*Oncorhynchus tshawytscha*) rearing in the north arm of the Fraser River estuary. Mar. Pollut. Bull. 22:20–26.

Levings, C. D., and R. B. Lauzier.
1991. Extensive use of the Fraser River basin as winter habitat by juvenile chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Zool. 69:1759–1767.

Linton, L. R., R. W. Davies, and F. J. Wrona.
1981. Resource utilization indices: an assessment. J. Animal Ecol. 50:283–292.

Macdonald, J. S., I. K. Birtwell, and G. M. Kruzynski.
1987. Food and habitat utilization by juvenile salmonids in the Campbell River estuary. Can. J. Fish. Aquat. Sci. 44:1233–1246.

McCabe, G. T., Jr., R. L. Emmett, W. D. Muir, and T. H. Blahm.
1986. Utilization of the Columbia River estuary by subyearling chinook salmon. Northwest Sci. 60:113–124.

Myers, K. W.
1980. An investigation of the utilization of four study areas in Yaquina Bay, Oregon, by hatchery and wild juvenile salmonids. M.S. thesis, Oregon State Univ., Corvallis, OR, 234 p.

Myers, K. W., and H. F. Horton.
1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. *In* V. S. Kennedy (ed.). Estuarine comparisons, p. 377–392. Academic Press, New York, NY.

Neilson, J. D., G. H. Geen, and D. Bottom.
1985. Estuarine growth of juvenile chinook salmon (*Oncorhynchus tshawytscha*) as inferred from otolith microstructure. Can. J. Fish. Aquat. Sci. 42:899–908.

Paszkowski, C. A., and B. L. Olla.
1985. Foraging behavior of hatchery-produced coho salmon (*Oncorhynchus kisutch*) smolts on live prey. Can. J. Fish. Aquat. Sci. 42:1915–1921.

Pearcy, W. G., and S. S. Myers.
1974. Larval fishes of Yaquina Bay, Oregon: a nursery ground for marine fishes? Fish. Bull. 72:201–213.

Peterman, R.
1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 41:1825–1829.

Peterson, W. T., R. D. Brodeur, and W. P. Pearcy.
1982. Food habits of juvenile salmon in the Oregon coastal zone, June 1979. Fish. Bull. 80:841–851.

Reimers, P. E.
1973. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Oreg. Fish. Comm. Res. Rep. 4(2), Oreg. Dep. Fish. Wildl., Portland, OR, 43 p.

Rogers, D. E., and G. T. Ruggerone.
1993. Factors affecting marine growth of Bristol Bay sockeye salmon. Fish. Res. 18:89–103.

Rondorf, D. W., and G. A. Gray, and R. B. Fairley.
1990. Feeding ecology of subyearling chinook salmon in riverine and reservoir habitats of the Columbia River. Trans. Am. Fish. Soc. 119:16–24.

Sagar, P. M., and G. J. Glova.
1987. Prey preferences of a riverine population of juvenile chinook salmon, *Oncorhynchus tshawytsch*. J. Fish Biol. 31:661–673.
1988. Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). J. Fish Biol. 33:643–653.

St John, M. A., J. S. Macdonald, P. J. Harrison, R. J. Beamish, and E. Choromanski.
1992. The Fraser River plume: some preliminary observations on the distribution of juvenile salmon, herring, and their prey. Fish. Oceanogr. 1:153–162.

Schoener, T. W.
1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418.

Shreffler, D. K., C. A. Simenstad, and R. M. Thom.
1992. Foraging by juvenile salmon in a restored estuarine wetland. Estuaries 15:204–213.

Simenstad, C. A., and R. C. Wissmar.
1984. Variability of estuarine food webs and production may limit our ability to enhance Pacific salmon (*Oncorhynchus* spp.). *In.* W. G. Pearcy ed.), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 274–286. Sea Grant College Program, Oregon State Univ., Corvallis, OR.

Simenstad, C. A., K. L. Fresh, and E. O. Salo.
1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. *In* V. S. Kennedy (ed.), Estuarine comparisons, p. 343–364. Academic Press, New York, NY.

Smirnov, B. P., V. V. Chebanova, and T. V. Vvedenskaya.
1994. Adaptation of hatchery-raised chum salmon, *Oncorhynchus keta*, and chinook salmon, *O. tshawytscha*, to natural feeding and effects of starvation. J. Ichthyol. 34:96–106.

Thomas, G. L., and O. A. Mathisen.
1993. Biological interactions of natural and enhanced stock of salmon in Alaska. Fish. Res. 18:1–17.

Wallace, R. K., Jr.
1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110:72–76.

Zaret, T. M., and A. S. Rand.
1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336–342.

Fish age determined from length: an evaluation of three methods using simulated red snapper data*

C. Phillip Goodyear

Miami Laboratory, Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive, Miami, Florida 33149

E-mail address: Phil_Goodyear@msn.com

Abstract.–The accuracy and precision of estimates of catch at age from sampled lengths were evaluated for three different methods with simulated red snapper, *Lutjanus campechanus*, data for 1984–94. The methods included a growth curve, age-length keys, and a probabilistic method to classify a known total number of fish into ages from samples of the length frequency of the catch. In the first method, ages were estimated from sample lengths directly from the growth curve. The second method involved expanding the sample length frequency to age frequency by using age-length keys. The probabilistic method incorporated the cumulative frequency distributions of length at age, year-class strength, and estimates of prior survival to build age probability distributions from sampled lengths. The evaluation was based on the error in the assigned catch at age and on the resulting estimates of numbers at age and fishing mortality arising from sequential population analysis. The probabilistic method was the best of the three for the situation evaluated here, and application of the age-length key was better than that of the growth model. However, the probabilistic method requires knowledge of growth, the distributions of size at age, and recruitment that may not be known, or only poorly so. Age-length keys require no such ancillary information and may be more practical in most situations, but the probabilistic method is superior if the data requirements can be met.

Manuscript accepted 31 July 1996.
Fishery Bulletin 95:39–46 (1997).

Age-structured stock-assessment methods require estimates of the age composition of the catch. In stock assessments for Gulf of Mexico red snapper, *Lutjanus campechanus*, age compositions are used that are estimated from the sampled size distribution of the catch with growth models (Goodyear[1]). The application of age-length keys developed from age determinations of length-stratified samples of the catch is a superior method (Ketchen, 1950; Hoenig and Heisey, 1987) that has been recently incorporated into the data collection program for this stock. However, it cannot be readily applied retroactively to improve the estimates of the age composition of historical catch, and it requires significantly more resources than the former method. In this paper, I compare the precision of the estimates of the age composition of the catch from these two methods with an alternative, using simulated red snapper data. The comparisons include both accuracy and precision of the estimates of the age composition of the catch and the consequent estimates of numbers at age and fishing mortality arising from their application to sequential population analysis following the methods of Gavaris [2] and Powers and Restrepo (1992).

Methods

Simulated data

The population simulation model used in this analysis (Goodyear, 1989) employed 30 discrete ages with an instantaneous annual natural mortality (M) of 0.2 for all ages in the fishery. Each year class was further partitioned into growth platoons (cohorts with identical age but different mean lengths). The position of a growth platoon in the distribution of size at age was fixed so that the larger individuals of a year class at age 1 remained larger throughout their lifetime. Mean lengths (L) at age (*A*) at the beginning of January were assumed to be equal to the estimates in the 1994 stock assessment for Gulf of Mexico red snapper (Goodyear[1]) and to correspond to the von Bertalanffy equation, $L=88.24(1-\exp(-0.159$

* Miami Laboratory Contribution MIA-94/95-42.

[1] Goodyear, P. 1994. Red snapper in U.S. waters of the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory, Miami, Admin. rep. MIA 93/94-63, 150 p.

[2] Gavaris, S. 1988. An adaptive framework for the estimation of population size. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 88/29, 4 p.

$(A+0.458))$, where L is total length in cm and A is age in years. Size at age in the absence of fishing mortality was assumed to be normally distributed with a coefficient of variation of length at age (v) of 0.10 based on the observed variability in size at age for red snapper (Goodyear[1]). The mean length of individuals of age a in growth platoon p, l_{ap}, was determined from mean size at age (L_a) by using the normal distribution and the coefficient of variation of length at age as

$$l_{ap} = L_a + L_a z_p v,$$

where: z_p is the standard normal deviate for the p^{th} percentile of the distribution. The simulation considered 101 growth platoons in each age class. The resulting distributions of lengths at the beginning of the year for ages 1–10 are shown in Figure 1. Within-year growth was evaluated as

$$W_{ap} = W_{a-1,p} \exp(G_{ap}),$$

where W_{ap} is the weight (kg) of an individual in growth platoon p at age a, and G_{ap} = instantaneous growth rate of growth platoon p at age a. The G_{ap} were estimated from lengths at age predicted from the von Bertalanffy growth equation.

The weight of a fish at capture W_c was evaluated as

$$W_c = W_{ap} Z_{ap} \left(\exp(G_a - Z_{ap}) - 1\right) / \left((G_{ap} - Z_{ap})(1 - \exp(-Z_{ap})\right),$$

where Z_{ap} is the total instantaneous mortality for growth platoon p at age a during the time period. Weight was converted to length with the length-weight equation ($W=1.158 \times L^{3.056}$, $r^2=0.985$, $n=25{,}375$) Growth, mortality, and catch were evaluated monthly.

The period simulated was from 1954 to 1994, but catch and sample data were retained and analyzed for 1984–94, which corresponds to the time span of actual data from the fishery. Recruitment in the model was specified by year class from 1954 to 1994 (Fig. 2). The values for 1972–94 follow the recruitment pattern observed in trawl surveys (Goodyear[1]). Earlier values were arbitrarily varied around the level observed at the beginning of the time series because landings from shrimp trawlers (predominantly juvenile fish) during these years were higher than those after 1972.

The value of fishing mortality in the model is the product of a maximum potential value for the year and a selectivity value based on the fish's age (Figs. 3 and 4). A dome-shaped selectivity schedule was

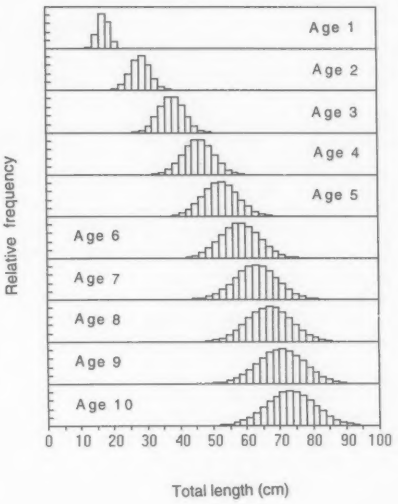


Figure 1

Simulated length-frequency distributions of red snapper, *Lutjanus campechanus*, at the beginning of the year for ages 1–10.

selected on the basis of age distribution of the catch (predominantly from handlines) in the 1994 assessment (Goodyear[1]). The value of the annual maximum for 1984–94 also follows the trend in the best estimates from the 1994 assessment, whereas earlier values were arbitrarily varied around the level observed at the beginning of the time series. The reduction in fishing mortality after 1990 was a response to management actions. The selectivity schedule (Fig. 4) was selected to produce a sample length frequency similar to that observed in the fishery (Fig. 5). Samples were truncated below 33 cm after 1990 to include the effects of changes in minimum size regulations at that time.

The simulated observations of length (and age) were obtained from the simulated catch. The catch from a growth platoon in the population structure was picked at random. It was evaluated for inclusion as an observation on the basis of the ratio of its magnitude (N_p) to the maximum catch from any other growth platoon (N_{max}). This was accomplished by drawing a uniform random number (R) between 0 and 1.0. If the ratio $N_p / N_{max} \geq R$, the length and age attributes of the cell were included as an observation; otherwise, they were discarded. This convention caused the sampled growth platoon to be proportional to their magnitude in the simulated catch. The process was repeated for each month of the simulation until 1,000 samples had been drawn. This provided 12,000 length

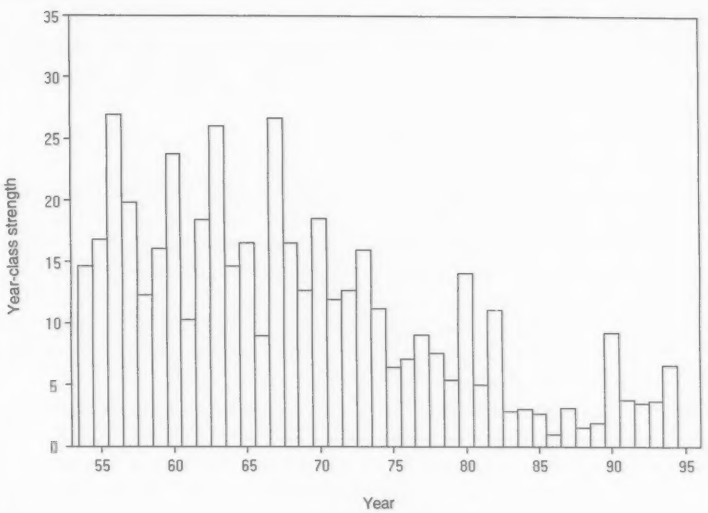


Figure 2

Recruitment history employed in the simulation. The values from 1972–94 are from trawl surveys.

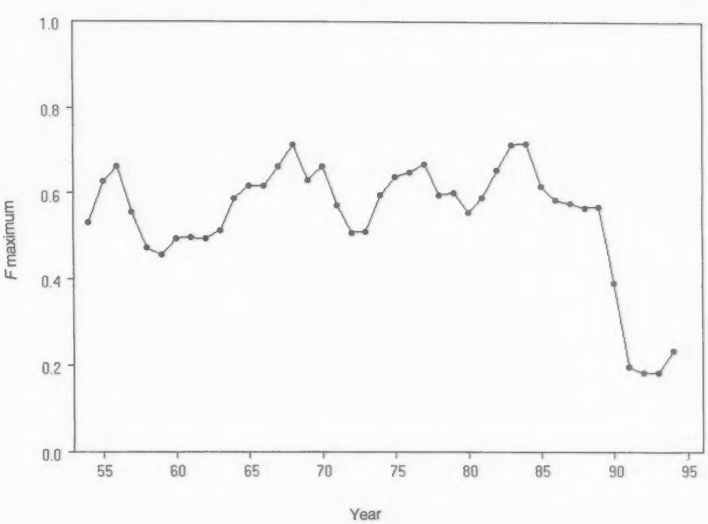


Figure 3

Maximum fishing mortality rates (F) used in the simulation, 1954–94.

samples per year. No error was added to either age or length to simulate measurement error.

The ages of the first two fish sampled in each 1-cm length stratum each month were retained with their lengths to build the age-length key for that month. This provided a maximum sample size of 24 fish per length stratum or about 4,000 fish per year to construct the age-length key, but sample size varied slightly because of the stochastic nature of the sampling process.

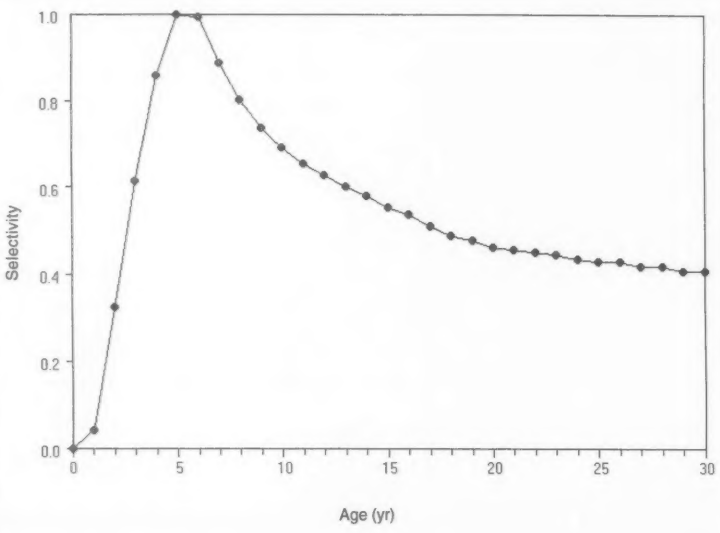


Figure 4

Selectivity schedule used in the simulation. The fishing mortality rate is the product of the maximum fishing mortality rate (F) and the selectivity value corresponding to fish age.

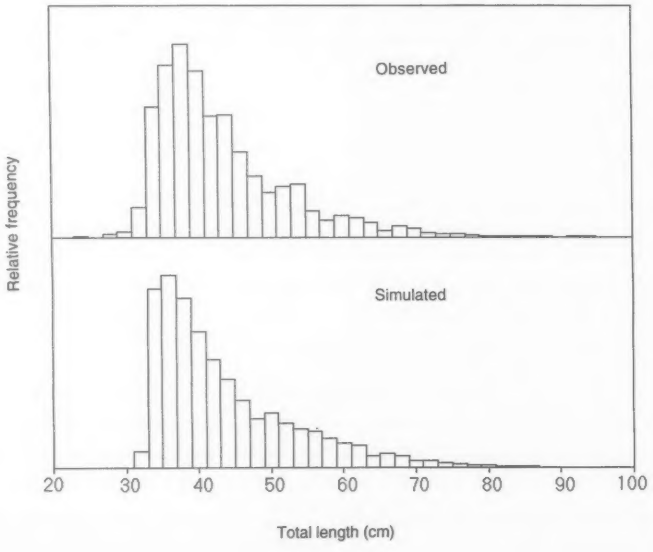


Figure 5

Observed and simulated length frequencies of red snapper harvested in 1993.

Age-estimation methods

For all three ageing methods evaluated, the number of fish in the catch at age a, N_a, was estimated as

$$N_a = Cf_a,$$

where C, the total catch in numbers of fish, was the known value from the simulation, and f_a was the estimated fraction of catch at age a. Age frequencies were estimated separately for each year between 1984 and 1994.

With the first method, the von-Bertalanffy growth equation was rearranged to predict age from length,

$$A = -\log_e(1 - L/88.24)/0.159 - 0.458,$$

and the f_a were estimated as the ratios of the number of sampled fish assigned age A to the total number of fish in the sample. For this method any sampled fish larger than the asympotic size was discarded.

With the second method typical age-length keys (Ketchen, 1950; Westrheim and Ricker, 1978) were constructed annually from the monthly age-frequency samples. In this case the f_a were estimated by multiplying the observed age frequencies for each length stratum by the ratio of length samples in each length stratum to the total number of length samples and by summing over ages.

The third (probabilistic) method is a proposed alternative and requires estimates of prior survival of year classes in the population and independent estimates of year-class strength. In this method

$$f_a = \frac{\sum_{i=1}^{j}\sum_{a=0}^{n} P_a}{j},$$

where j is the number of length samples, n is the number of ages, and

$$P_a = \frac{W_a R_{y-a} S_a}{\sum_{a=1}^{n} W_a R_{y-a} S_a}$$

and

$$W_a = \frac{dD_a}{dL_i},$$

where D_a is the cumulative probability distribution of length for age a, L_i is the observed length of fish i, R_{y-a} is the recruitment strength in year y–a, y is the year of observation, and S_a is survival probability from recruitment to age a and is given by

$$S_a = \exp\sum_{i=0}^{a-1} -(F_i + M_i),$$

where F_i is the fishing mortality of the year class at age a when it was age i, and M_i is the natural mortality of the year class at age a when it was age i.

Inspection of the data used in this method reveals that the method requires values for nearly everything one would wish to estimate from the age composition of the catch and consequently seems to place the cart before the horse. However, in many cases ancillary data on year-class strength may be available from research surveys, and estimates of natural and fishing mortalities may be available from earlier assessments. In this investigation, this method was applied in two ways. The first assumed preexisting accurate knowledge of year-class strengths and mortality. The second application assumed knowledge of year-class strengths and natural mortality and proceeded iteratively. In the first iteration, age composition was estimated with the assumption that there was no fishing mortality. This led to a set of estimates of catch at age that were then used through sequential population analysis to estimate fishing mortality at age. With the second iteration the resulting estimates of fishing mortality were added and catch at age was reestimated. This process was repeated several additional times.

Overall, the three methods provided 4 sets of estimates of catch at age that could be compared with the true values from the simulation: those from the growth model, those from the age-length key, those from the probabilistic method given knowledge of survival, and those from the iterated probabilistic method. In addition, numbers at age and fishing mortality for each year were estimated from the catches at age for each set by using sequential population analysis (Powers and Restrepo, 1992). For the purpose of this exercise, the selectivities for the terminal year of the population analysis were the known values from the simulation, and the tuning index was the known number of age-4 individuals alive at the beginning of the year. The methods were compared by correlating the known true values from the simulation to the values estimated by each method. Because there were 31 ages in the model (0–30) and 11 years, these provided a total maximum sample size of 341; however, year-age combinations where the true catch at age was below 100 were dropped. Thus sample sizes for most analyses were reduced to 331. In addition, scattergrams of the logs of the ratios of estimated to true values were constructed for each comparison. The r^2 values for the correlations between true and estimated values are presented with

each of the scattergrams. Although the scattergrams involve transformations to reflect the error more accurately, the correlations themselves are based on the untransformed data.

Results

The estimates of catch at age from each of the methods were highly correlated with the true values (Fig. 6). But the error in catch at age was clearly highest for the ages assigned with the growth model (Fig. 6A). Catch at age from the age-length key was considerably better than that from the growth model, particularly for the younger more abundant ages in the catch (Fig. 6B). The younger ages in these figures tend to be to the right side of the scattergrams and the older, less abundant ages are on the left.

The probabilistic method, given prior knowledge of fishing mortality and recruitment, provided the best result, with very little difference between true and estimated age compositions except at the oldest ages (Fig. 6C). The bias in the estimates obtained with this method with only natural mortality is evident in Figure 6D, but even so, the estimates for the youngest ages are better than the estimates from the growth model. The bias was reduced by the fifth iteration (Fig. 6E) and almost completely removed by the tenth iteration (Fig. 6F).

The estimates of number at age derived from each set of catch at age by using an age-sequenced analysis are presented in Figure 7. Again the results were least favorable for the catch-at-age matrix developed from the growth model (Fig. 7A), followed by the age-length key (Fig. 7B) and the probabilistic method (Fig. 7C). The bias in estimated number at age from the probabilistic method, where fishing mortality is not used, is even more pronounced than it was for the catch-at-age matrix (Figs. 5D and 6D). However, the bias was reduced by the fifth iteration by using the fishing mortality rates derived from prior iterations and almost completely removed by the tenth iteration (Fig. 7, E–F). The similarity of r^2 values for the correlations between observed and predicted values for the age-length key and probabilistic methods in Figures 6 and 7 are somewhat misleading because of the very large dynamic range of the numbers and corresponding catches at age used in the analysis. In actuality, the precision of the estimates arising from applicaton of the age-length key was much lower than that for the probabilistic method for age classes that were infrequent in the catch.

The estimates of fishing mortality at age, derived from each set of catch at age by using age-sequenced

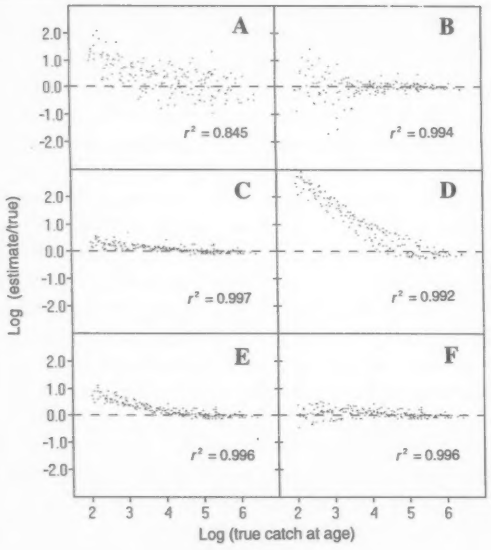


Figure 6

Ratios of estimated to true catch at age from the growth model (**A**), age-length key (**B**), and from the probabilistic method with knowledge of prior survival (**C**), and probabilistic iterations 1, 5 and 10 (**D–F**).

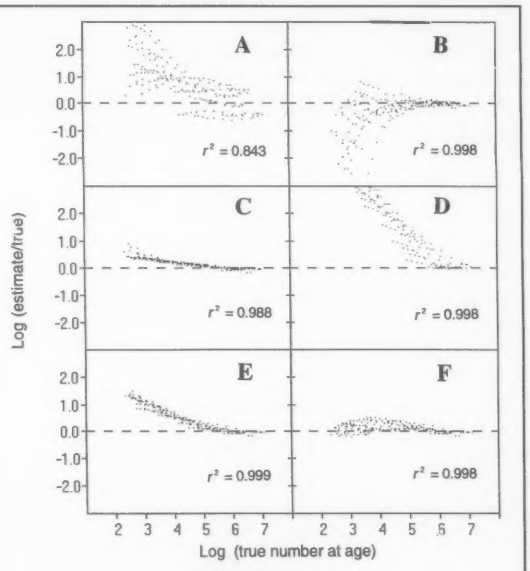


Figure 7

Ratios of estimated to true number at age from analysis of catch at age from the growth model (**A**), age–length key (**B**), probabilistic method with knowledge of prior survival (**C**), and probabilistic iterations 1, 5 and 10 (**D–F**).

analysis, are presented in Figure 8 for ages up to 10. Again, the results were least favorable for the catch-at-age matrix developed from the growth model (Fig. 8A), followed by the age-length key (Fig. 8B), and the probabilistic method (Fig. 8C). The upward bias in estimated number at age from the probabilistic method in the absence of fishing mortality in Figure 7D led to an underestimate of fishing mortality of Figure 8D. However, the bias was reduced by the fifth iteration and almost completely removed by the tenth iteration (Fig. 8, E–F).

The relatively higher error in the catch at age for older ages estimated by using the growth model and age-length key (Fig. 6, A–B) led to relatively higher error in the estimates of numbers at age from their analysis. This resulted in poor estimation of fishing mortality for the oldest ages in the simulated catch which caused the correlation between true and estimated fishing mortalities to decline when fish older than 10 years were included in the analysis (Fig. 9, A–B). The results from the probabilistic approach also showed a similar trend but were much less sensitive than those for the other two methods (Fig. 9, D–F).

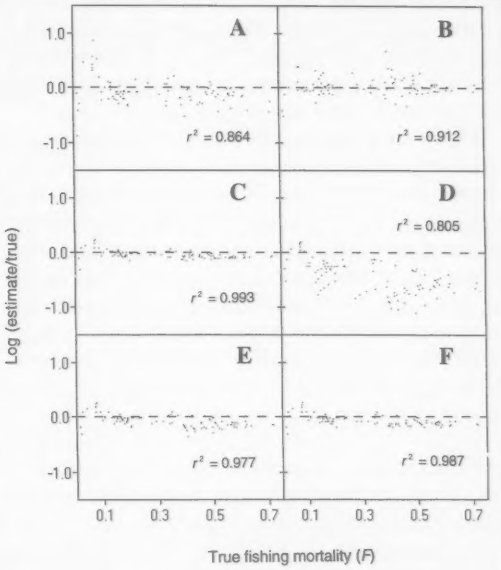


Figure 8

Ratios of estimated to true fishing mortality (F) from analysis of catch at age from the growth model (**A**), age-length key (**B**), probabilistic method with knowledge of prior survival (**C**), and probabilistic iterations 1, 5, and 10 (**D–F**).

Discussion

These results indicate that for the situation evaluated here the probabilistic method is superior to age assignment from either a growth model or an age-length key. Factors leading to this conclusion include knowledge of the actual history of year-class strengths and perfect knowledge of growth, natural mortality, and the distribution of size at age. Imperfect knowledge of any of these elements would degrade the performance of the probabilistic method. If there are sufficient data to develop a growth curve then it should be possible to characterize the distribution of size at age, at least for the more abundant ages in the population. Poor knowledge of the growth curve itself would also adversely affect the estimates obtained directly from the growth curve.

The results from the age-length key would be unaffected by poor knowledge of growth, past recruitment, and natural mortality. However, the comparisons among methods in the current analysis assumed no error in age assignments for the age-length key. Experience suggests that there is uncertainty in age assignment from hard-part analysis, an uncertainty that increases with fish age (Beamish and Fournier, 1981). Including such error would have added to the difference between the results of this method and those obtained with the probabilistic method. Nonetheless, the construction and application of age-

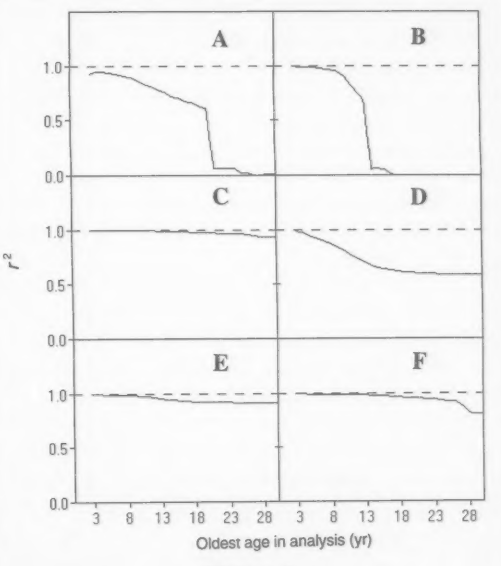


Figure 9

Precision of fishing mortality estimates (r^2 from correlations of true and estimated rates) from the growth model (**A**), age-length key (**B**), probabilistic method with knowledge of prior survival (**C**), and probabilistic iterations 1, 5, and 10 (**D–F**).

length keys involves the fewest assumptions. Where almost certain knowledge of growth and year-class strengths is lacking, and the method for ageing the fish is robust, this method is probably the best choice for monitoring the age composition of a catch.

Where time-series data for year-class strengths are available, where growth and natural mortality are reasonably known, and where there are insufficient age determinations to construct age-length keys, the probabilistic method is clearly superior to age assignments from inverted growth models and also might be as good as, or better than, the age-length keys if they were available. Where growth and year-class strengths are well characterized and natural mortality is reasonably known, the probabilistic method should outperform all the other alternatives. Additionally, this method should be very useful for estimating the age composition of catches for the most recent year of a time series for which sample-age analysis may not yet be complete. It should also provide a reliable method to estimate the age compositions of catches for intermediate years of a time series, for which insufficient age determinations are available to construct age-length keys.

Acknowledgments

I thank M. Schirripa, C. Porch, and two anonymous reviewers for helpful comments on the manuscript.

Literature cited

Beamish, R. J., and D. A. Fournier.
1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982–983.

Goodyear, C. P.
1989. LSIM-A length-based fish population simulation model. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC-219.

Hoenig, J. M., and D. M. Heisey.
1987. Use of log-linear model with the EM algorithm to correct estimates of stock composition and to convert length to age. Trans. Am. Fish. Soc. 116:232–243.

Ketchen, K. S.
1950. Stratified subsampling for determining age-distributions. Trans. Am. Fish. Soc. 79:205–212.

Powers, J. E., and V. R. Restrepo.
1992. Additional options for age-sequenced analysis. Int. Comm. Conserv. Atl. Tunas Coll. Vol. Scientific Papers 39(2):540–553.

Westrheim, S. J., and W. E. Ricker.
1978. Bias in using an age-length key to estimate age-frequency distributions. J. Fish. Res. Board Can. 35:184–189.

The life history and stock separation of silver kob, *Argyrosomus inodorus*, in South African waters

Marc H. Griffiths

Sea Fisheries Research Institute
Private Bag X2, Roggebaai 8012, Cape Town, South Africa

and

Department of Ichthyology and Fisheries Science, Rhodes University
P.O. Box 94, Grahamstown 6140, South Africa

E-mail address: mgriffith@sfri.sfri.ac.za

Abstract.—Fishery dependent and fishery independent distribution analyses together reveal that there are three discrete areas of *Argyrosomus inodorus* abundance between Cape Point and the Kei River: one in the southeastern Cape, one in the southern Cape, and one in the southwestern Cape. On the basis of migratory patterns determined from tagging and catch data, differences in growth rates, otolith-dimension and fish-length relationships, growth zone structure, sizes at maturity and sex ratios, and on the fact that each region has nursery and spawning areas, the conclusion has been drawn that these areas of abundance represent three separate stocks. Each stock apparently disperses offshore in winter (to ca. 100 m depth) and concentrates nearshore in summer (<60 m depth) in response to oceanographic patterns. Although there is evidence of spawning activity throughout the year, the main spawning season for silver kob is from August to December, with a peak in spring (Sep–Nov). Size at sexual maturity for silver kob was smaller in the southeastern Cape than in the southern Cape, and in both regions males matured before females. Median sizes at maturity (L_{50}) for females and males were 310 mm TL (1.3 yr) and 290 mm TL (1 yr) respectively in the southeastern Cape and 375 mm TL (2.4 yr) and 325 mm TL (1.5 yr) respectively in the southern Cape. East of Cape Agulhas, *A. inodorus* are found just beyond the surf zone to depths of 120 m. Adults occur predominantly on reefs (>20 m), whereas juveniles are found mainly over soft substrata of sand or mud (5–120 m depth). Young juveniles recruit to nurseries immediately seaward of the surf zone (5–10 m depth) but move deeper with growth. Because of lower water temperatures west of Cape Agulhas, the adults in this area are found from the surf zone to depths of only 20 m in summer.

Manuscript accepted 22 August 1996.
Fishery Bulletin 95:47–67 (1997).

Silver kob, *Argyrosomus inodorus*, is an important commercial and recreational sciaenid fish (max. size 34 kg) that is known from northern Namibia on the west coast of southern Africa to the Kei River on the east coast of South Africa (Griffiths and Heemstra, 1995). It is not common between Cape Point and central Namibia; therefore it is likely that the Namibian populations are not continuous with those off the eastern seaboard of South Africa (Griffiths and Heemstra, 1995). Until recently *A. inodorus* was misidentified as *A. hololepidotus* throughout its distribution; off South Africa it was also confused with a sympatric species, *A. japonicus* (Griffiths and Heemstra, 1995).

The South African line fishery consists of about 2,900 commercial (Kroon[1]) and some 4,000 club-affiliated recreational (Ferreira, 1993) vessels. These vary from 5 to 15 m in length and operate on both east and west coasts. Silver kob is probably the most valuable species caught by the line fishery between Cape Point and East London if market value and annual catch are combined; *A. inodorus* is also landed as a bycatch of the sole- and hake-directed inshore trawl fishery between Cape Agulhas and Port Alfred (Japp et al., 1994) and is caught by rock and surf anglers and commercial beach-seine fishermen in the southwestern Cape. Although an important species, trawl and line catch per unit of effort for this species has declined substantially during the last three decades, and concern has been expressed over the large contribution of recruits to line catches in the southeastern Cape (Smale, 1985; Hecht and Tilney, 1989).

Knowledge of the life history of fishes "is an almost essential prerequisite to successful identification of stocks" (Pawson and Jennings, 1996) and is fundamental to stock assessment and to the formulation of effective management strategies for their sustainable use. Despite the importance of *A. inodorus* and evidence for declining catches, little has been published on its life history; wise management has therefore not been possible. Smale (1985) investigated the sex ratio and spawning seasonality of "*A. hololepidotus*" based on the catches of lineboat fishermen in Algoa Bay but inadvertently included both *A. inodorus* and *A. japonicus* in his study (established via voucher specimens and otoliths). Griffiths (in press, a) recently described the growth of *A. inodorus* from three geographical regions between Cape

[1] Kroon, W. 1995. Sea Fisheries, Permit Division, P. Bag X2, Roggebaai, 8012, Cape Town, South Africa. Personal commun.

Point and the Kei River. On the basis of grow rate, fish-length and otolith-dimension relationships, and the appearance of growth zones, he concluded that silver kob within this area comprise at least three separate stocks.

The objective of the present study was to provide information on the life history of *A. inodorus* occurring between Cape Point and the Kei River, including reproductive seasonality, spawning grounds, size at maturity, juvenile and adult distribution, and migration. Because the identification of discrete stocks or "management units" is essential for effective management (Pawson and Jennings, 1996), the multiple stock concept is further developed with information on distribution and abundance, life history parameters, and mark-recapture data.

Materials and methods

The study area (from Cape Point to Kei River) was divided into three regions for sampling purposes (Fig. 1). These regions were identical to those used by Griffiths (in press, a); they were not divided according to political boundaries but rather generated to increase analytical resolution. Biological (March 1990–January 1992) and length-frequency (January 1990–December 1994) data were collected in each region from fish caught 1) by the line fishery, 2) by the inshore trawl fishery, 3) by trawlers during South Coast Biomass Surveys conducted by the Sea Fisheries Research Institute, and 4) by research linefishing operations. Biological data were also obtained from silver kob caught by beach seines in False Bay (Oct 1991). Trawled fish were generally caught over sand or mud substrata, and line-caught fish over reef. Owing to the high relief rocky nature of the inshore habitat west of Cape Agulhas, this species is not trawled in the southwestern Cape.

Fish sampled for biological purposes were measured (to the nearest 1 mm [total length]), weighed (to the nearest gram [fish <500 g], the nearest 20 g [fish 500 g–5 kg], or the nearest 100 g [fish 5 kg–25 kg]), cut open, and sexed. Gonads were removed, assigned a visual index of maturity (see Table 1), and weighed to the nearest 0.1 g. Males were assigned an index of drumming muscle development (1=none, 2=partially developed, 3=fully developed). Owing to logistical constraints, monthly biological data were obtained only for the southeastern Cape; in the other two regions biological sampling was limited to the spawning season.

Areas of silver kob abundance were delineated by using returns from the commercial line fishery and data from South Coast Biomass Surveys (SCBS's). Line catches consisted predominantly of adult fish, whereas trawl catches from SCBS's comprised mostly juveniles and young adults (see below). Annual catch-per-unit-of-effort data (catch per outing) were plotted on a subregional basis for the commercial line fishery (an outing did not exceed one day), and the data from 14 SCBS's (Table 2) were used to calculate

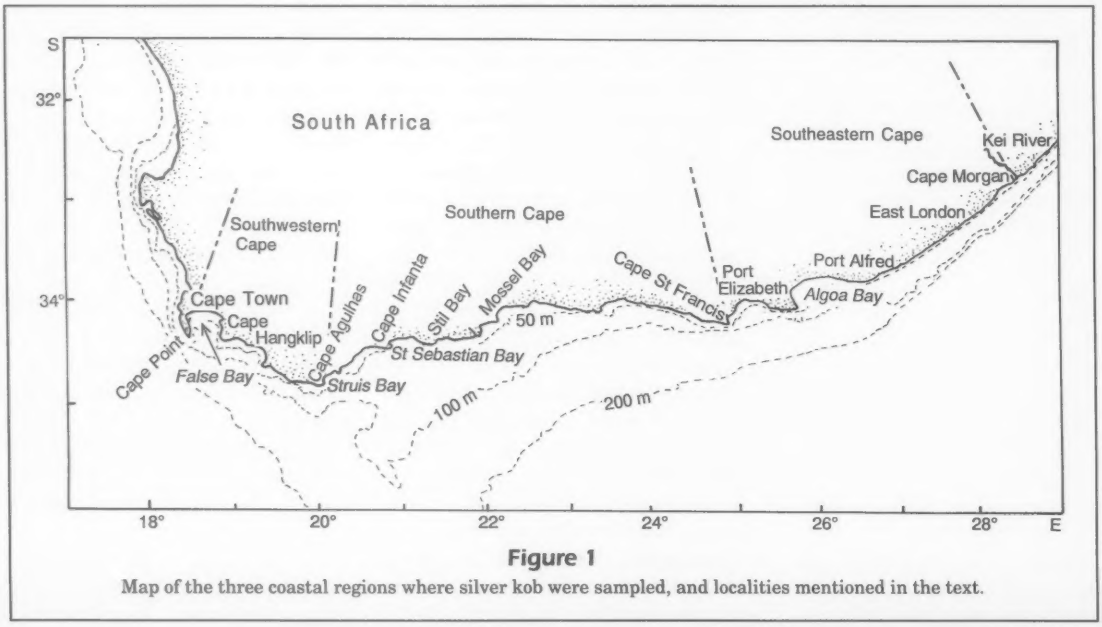


Figure 1

Map of the three coastal regions where silver kob were sampled, and localities mentioned in the text.

Table 1

Classification and description of the macroscopic gonad maturity stages of *Argyrosomus inodorus*.

Stage		Description
1	**Juvenile**	This stage is generally only found in fish < 200 mm TL. Testes are threadlike, and the ovaries appear as transparent pinkish flaccid sacs, about half the length of those at stage 2.
2	**Immature or resting**	Testes are extremely thin, flat, and pinkish white. Ovaries appear as translucent orange tubes. Eggs are not visible to the naked eye.
3	**Active**	Testes are wider, triangular in cross section and beige. Sperm are visible if the gonad is cut and gently squeezed. Eggs become visible to the naked eye as tiny yellow granules in a gelatinous orange matrix. There is very little increase in the diameter of the ovary.
4	**Developing**	Testes become wider and deeper and are mottled and creamy beige. They are also softer in texture, rupturing when lightly pinched. Besides the obvious presence of sperm in the main sperm duct, some sperm are also present in the tissue. Ovaries become larger in diameter and opaque yellow in color. Clearly discernible eggs occupy the entire ovary.
5	**Ripe**	Testes still larger in cross section and softer in texture. They become creamier in color owing to considerable quantities of sperm. The ovaries are larger in diameter as a result of an increase in egg size.
6	**Ripe and running**	Testes even larger in cross section and uniformly cream in color. They are extremely delicate at this stage and rupture easily when handled. Sperm are freely extruded when pressure is applied to the abdomen of the whole fish. Ovaries amber in color and have a substantial proportion of hydrated eggs.
7	**Spent**	Testes are shrivelled and a mottled beige and cream. A little viscous semen may still ooze from the genital pore when pressure is applied to the abdomen. Ovaries are reduced in size, similar in appearance to those at stage 2 and have a few remaining yolked oocytes. These yolked oocytes are generally aspherical and appear to be undergoing resorption.

mean numbers of silver kob per 30-min trawl per grid block. The SCBS methods are fully described by Badenhorst and Smale (1991); therefore only a summary is given here. The survey area extended from Cape Agulhas to Port Alfred and seawards to a depth of 500 m. This area was divided into four depth zones (0–50 m, 51–100 m, 101–200 m, and 200–500 m), which were in turn subdivided into blocks of 5 × 5 nautical miles. The blocks trawled during each survey were determined semirandomly according to the ratio of blocks per stratum. Bobbins were not used; therefore trawling was limited to nonreef substrata. The shallowest depth over which the research vessel (*F.R.S. Africana*) could operate was 20 m. A 180-ft German trawler with a 25-mm-mesh (bar) liner attached to the trawl bag was used. Trawl duration was limited to 30 min, and the results of shorter trawls (owing to technical reasons or to hitting the reef) were standardized to that time. Bottom temperature was recorded immediately after most trawls with a Neil Brown MK III-B conductivity, temperature, and depth probe (CTD). Mean numbers of *A. inodorus* per trawl for each 1°C of bottom temperature were plotted to obtain the preferred temperature range of this species.

Migration of *A. inodorus* was studied by using tagging and catch data. A tagging program was initiated in February 1994. Silver kob captured with hook and line were tagged with plastic T-bar tags in False Bay (n=1,034), off Struis Bay (n=750), and off Stil Bay (n=291). The data for recaptured silver kob

Table 2

Number of trawls in which juvenile *A. inodorus* were caught during South Coast Biomass Surveys between Cape Agulhas (20°E) and Port Alfred (27°E) during the period 1987–95.

Cruise	Total trawls	Trawls with silver kob
9 Sep–4 Oct 1987	88	24
11 May–2 Jun 1988	93	8
11 May–28 May 1989	62	12
24 May–12 Jun 1990	58	12
8 Sep–26 Sep 1990	73	21
8 Jun–1 Jul 1991	91	24
14 Sep–2 Oct 1991	75	30
1 Apr–20 Apr 1992	82	6
3 Sep–20 Sep 1992	87	32
19 Apr–10 May 1993	109	9
2 Sep–28 Sep 1993	106	30
8 Jun–3 Jul 1994	89	11
22 Sep–16 Oct 1994	92	18
23 Apr–15 May 1995	95	9
All cruises	1,200	246

(n=157), predominantly adults, were analyzed according to tagging locality, days free, and the minimum aquatic distance travelled.

Owners of commercial line boats and inshore trawlers are required to submit daily catch returns to the Sea Fisheries Research Institute. The monthly catches of *A. inodorus* made by commercial linefishermen in each of the three regions and the monthly catches made by the inshore trawl fishery in the southern Cape and the southeastern Cape for the period 1986–94 were expressed as percentages of the respective annual totals.

The median size at first maturity (L_{50}) for males and females was estimated by fitting a logistical function (LOGIT) to the fractions of mature fish (gonad stage 3+) per 50-mm length class (midpoint) that were sampled in the southern Cape and the southeastern Cape during the breeding season. Many of the smaller males with active testes lacked drumming muscles. Logistical functions were therefore also fitted to the fractions of males (per 50-mm length class) with fully developed drumming muscles. Because *A. inodorus* are not trawled in the southwestern Cape, few juveniles were sampled and L_{50} values could not be calculated for that region.

Reproductive seasonality was established in the southeastern Cape by calculating both gonadosomatic indices (GSI's) and the monthly percent frequency of each maturity stage for fish $>L_{50}$.

$$\text{GSI} = \text{gonad weight}/(\text{fish weight} - \text{gonad weight}) \times 100.$$

The extent of the spawning area was determined by computing the percent frequency of each maturity stage for fish ($>L_{50}$) that were sampled during peak spawning (Oct and Nov 1991) off East London, Port Alfred, Mossel Bay, St Sebastian Bay, and False Bay. Sex ratios were tested statistically for significant deviations from unity with a chi-square test (P<0.05).

Nursery areas were delineated by comparing the length-frequency distributions of silver kob caught 1) during South Coast Biomass Surveys (SCBS), 2) during experimental linefishing expeditions (no minimum size) and 3) by the line fishery (1990–94) as well as by analyzing the catch and effort distributions generated for silver kob during SCBS's (1987–95).

Results

Catch distribution and migration

Geographically related catch and CPUE trends for the line fishery consisted of three modal groups (Fig. 2), indicating that there are three areas of adult abundance between Cape Point and the Kei River (one in each region). Data from SCBS's showed that adult abundance trends were reflected in juvenile distribution, at least for the east coast (Fig. 3). Substantial differences in growth rates, otolith-dimension and fish-length relationships, and growth zone structure (Griffiths, in press, a) suggest that these areas of abundance represent three allopatric stocks. Tag returns from the present study revealed that South African silver kob are capable of migrations of 240 km in six months but that most fish (84%) did not move more than 50 km from their tagging locality (Fig. 4). Only one fish tagged in False Bay was recaptured outside of that bay. Of the silver kob tagged in the Struis Bay vicinity, five (5.3%) had migrated westwards to False Bay, and the rest were recaptured either within 50 km of the tagging locality (77.3%) or had moved eastwards (17%), but only as far as Mossel Bay. None of the tagged fish were recaptured in the southeastern Cape. Tagging data therefore support the three-stock concept but suggest that there is limited exchange between silver kob in the southern Cape and those in the southwestern Cape. Based on catch data, the foci of each stock are apparently False Bay, Stil Bay, and Port Alfred, which are separated by distances of 396 and 630 km, respectively. Struis Bay is situated towards the westerly extreme of the area occupied by the southern Cape stock: therefore it is not surprising that of the recaptured silver kob that had moved substantial distances (>50 km) from this tagging locality, most had moved to the east.

Interviews with commercial linefishermen ([n=36]; also confirmed by author's personal experience) indicated that their silver kob catch was made on reefs at depths of 20–60 m to the east and 5–20 m to the west of Cape Agulhas. Inshore trawling between Cape Agulhas and Port Alfred occurs on soft ground at depths of 50–120 m (Japp et al., 1994). Decreases in the line catches of all three stocks during winter (Fig. 5) and corresponding increases in the catches made by inshore trawlers (Fig. 6) suggest that silver kob move farther offshore at this time of the year. Because inshore trawlers fish over substrata that are different from those over which linefishermen fish and since they land mostly juvenile and young adult *A. inodorus* (Fig. 7), it could be argued that trawl catch data do not reflect the winter locality of the adult population. The offshore movement of adults is supported, however, by the recapture of four specimens (435–720 mm) tagged in 30 m of water off Struis Bay in summer 1995 by inshore trawlers operating in 80 m off Stil Bay and off Cape Infanta in the winter and early spring of that year. Presumably, large adults

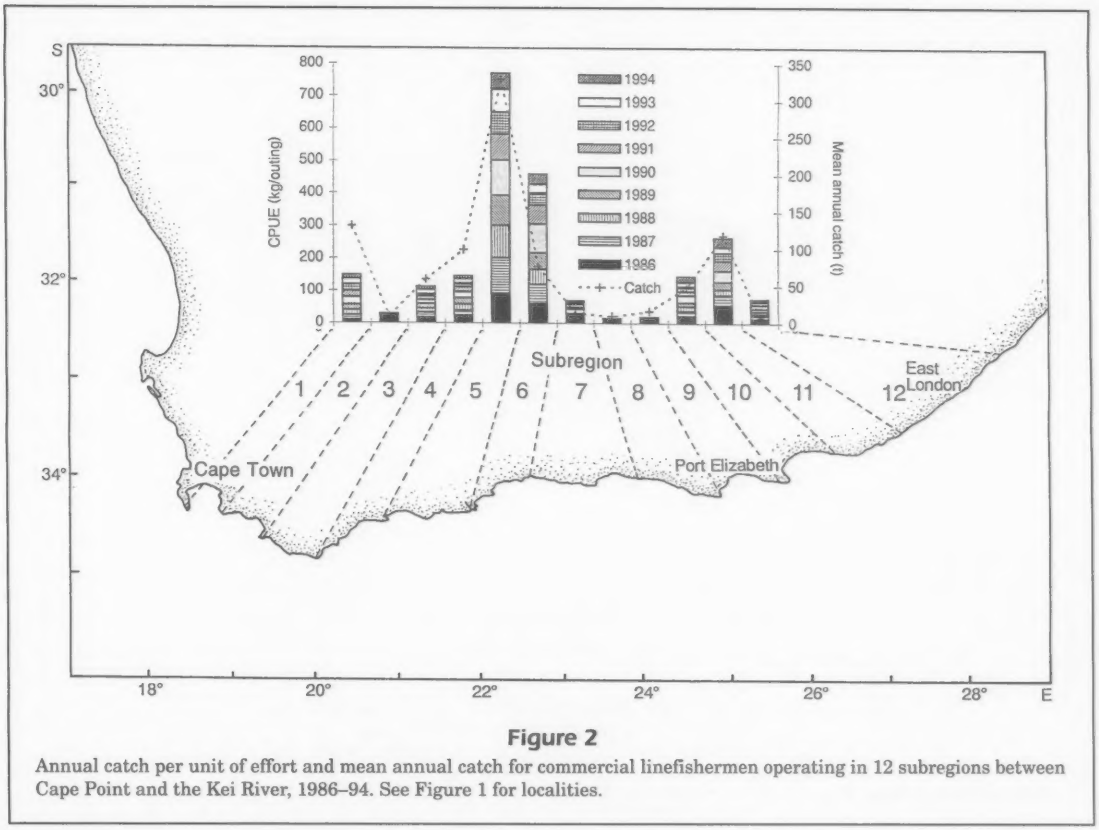


Figure 2

Annual catch per unit of effort and mean annual catch for commercial linefishermen operating in 12 subregions between Cape Point and the Kei River, 1986–94. See Figure 1 for localities.

are also found on predominantly untrawlable rocky substrata during their offshore winter distribution.

Size at maturity

Silver kob were found to mature at a smaller size in the southeastern Cape than in the southern Cape, and in both regions males matured at a smaller size than did females. Females began to mature at about 250 mm in both regions, but the percentages of mature fish in consecutive size classes increased more rapidly in the southeastern Cape than in the southern Cape (Fig. 8, A and B). Estimated median lengths at maturity (L_{50}) were 310 mm and 375 mm for the two regions respectively. All females in the southeastern Cape larger than 450 mm and all females in the southern Cape larger than 550 mm were mature (Fig. 8, A and B).

A comparison of the testes method with the drumming muscle method for estimating male maturity indicated that, within each region, the two methods produced similar estimates for length at total maturity but that the testes method produced higher estimates for the proportions of mature fish in size classes below this length. In the southeastern Cape, males began to mature at 150 mm (testes method) and at 200 mm (drumming muscle method), L_{50} was calculated at 205 mm (testes method) and 290 mm (drumming muscle method), and total maturity was attained at 400 mm (both methods)(Fig. 8, C and E). In the southern Cape, males began to mature at 200 mm (testes method) and at 250 mm (drumming muscle method), L_{50} was calculated at 270 mm (testes method) and 325 mm (drumming muscle method), and total maturity was attained at 450 mm (both methods)(Fig. 8, D and F).

Many of the smaller males (<300 mm) classified as mature (i.e. testes contained sperm), had disproportionately smaller gonads and also lacked drumming muscles. Because male drumming plays an important role in sciaenid spawning behavior (Takemura et al., 1978; Saucier and Baltz, 1993; Connaughton and Taylor, 1995; Connaughton, 1996), it is not known whether these fish would actually spawn. Even if the small males (without drumming muscles) managed to spawn with a communal spawn-

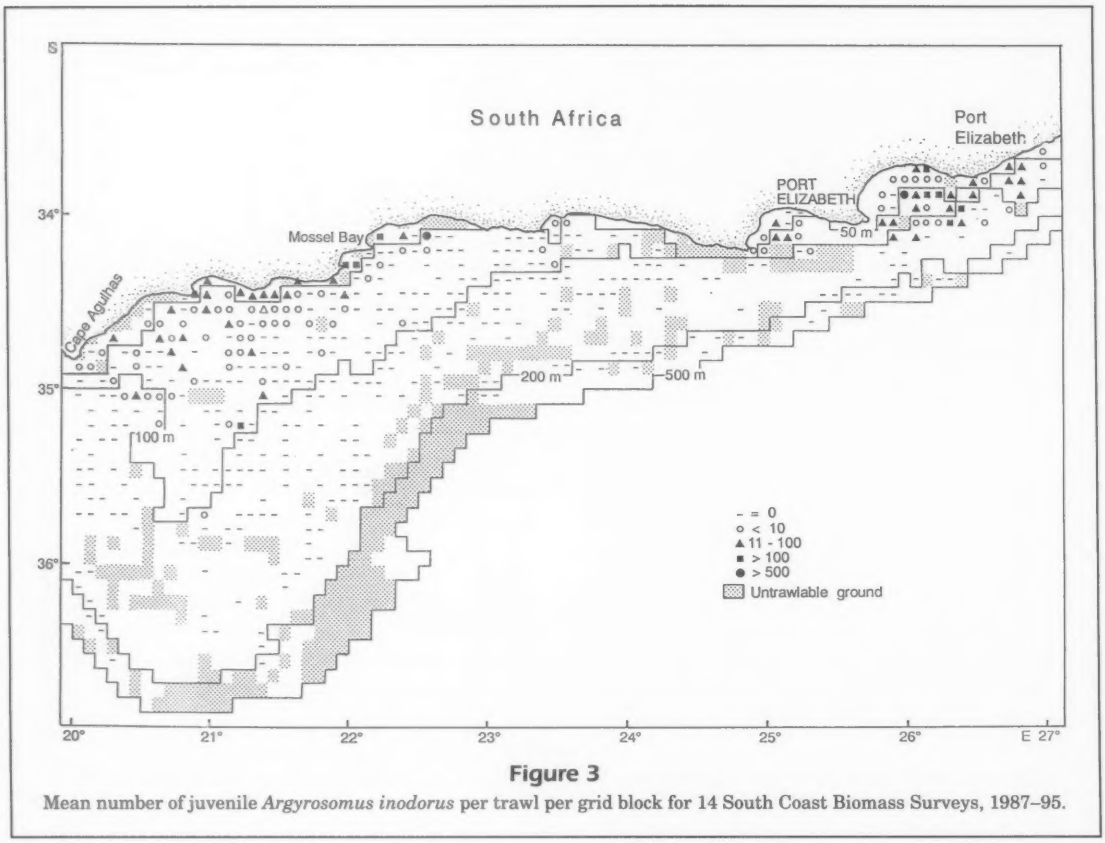


Figure 3

Mean number of juvenile *Argyrosomus inodorus* per trawl per grid block for 14 South Coast Biomass Surveys, 1987–95.

ing aggregation (doubtful as this may be), their contribution to the total reproductive output (of the aggregation), in relation to the small size of their testes, would likely be extremely low. Therefore, from a management view point, the L_{50} estimates based on drumming muscle development were regarded as more useful than those based on gonad staging.

According to Griffiths (in press, a), there was no difference between the growth rates of *A. inodorus* in the southeastern Cape and those in the southern Cape during 1990–91. The smaller sizes at maturity in the former region were therefore due to earlier maturity and not to slower growth. Female L_{50} and total maturity are attained at about 1.3 and 3.5 yr in the southeastern Cape and at about 2.4 and 4.7 yr in the southern Cape. Male L_{50}, based on testes staging and on drumming muscle development, was attained at <1 yr and at 1 yr for silver kob in the southeastern Cape, and at <1 yr (testes staging) and at 1.5 yr (drumming muscle development) in the southern Cape. Total male maturity was attained at about 2.8 yr in the southeastern Cape and at about 3.4 yr in the southern Cape.

Spawning

Gonadosomatic indices (Fig. 9) and gonad maturity indices (Fig. 10) for silver kob in the southeastern Cape showed that although some spawning occurred throughout the year, there was a clearly defined breeding season from August to December and that peak spawning occurred in spring (Sep–Nov). These results are in general agreement with those of Smale (1985) for Algoa Bay, but his spawning season appears to have been "extended" by about one month, through the inclusion of *A. japonicus*, which spawns from October to January (Griffiths, in press, b) in the southeastern Cape. The low proportion of ripe and running (stage-6) females sampled during the spawning season (Fig. 10; and Smale, 1985) suggests that females feed less and are therefore less prone to capture (with hook and line) after oocyte hydration. This inference is supported by a much higher proportion of stage-6 females in catches of silver kob caught by beach seines in False Bay than in catches made by using hook and line in four other localities

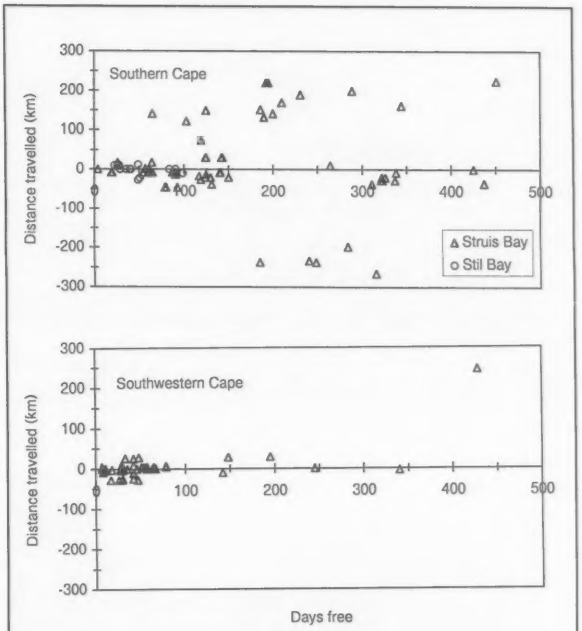


Figure 4

Minimum distance travelled versus days at liberty for recaptured *Argyrosomus inodorus* that were tagged in the southern Cape and in the southwestern Cape (False Bay), South Africa (1994–96). Positive values signify a coastwise migration to the east, and negative values a movement to the west.

(during similar months and times of day)(Fig. 11). Very low numbers of females with hydrated oocytes have also been reported in line catches of other sciaenids, e.g. *Sciaenops ocellatus* (Fitzhugh et al., 1988), *Micropogonias undulatus* (Barbieri et al., 1994), and *Atractoscion aequidens* (Griffiths and Hecht, 1995a); no hydrated oocytes were detected from line catches of *Argyrosomus japonicus* (Griffiths, in press, b). Most silver kob caught during SCBS's were juveniles. Nevertheless, none of the adult females that were trawled had hydrated oocytes, perhaps because these fish were captured on the nursery grounds and not on adult habitat where spawning is expected to occur (see below).

The large proportion of ripe and ripe and running (stages 5 and 6) males and females at each of the five sites between Cape Point and the Kei River (Fig. 11) during October–November suggests that spawning occurs throughout the study area and that peak spawning occurs during spring for all three stocks. The inshore distribution of the adults during spring and summer, the absence of *Argyrosomus* eggs and larvae in the Agulhas Current (ca. 200 m)(Beckley, 1993), and the occurrence of significant numbers of early stages of *A. inodorus* larvae (identified as "*A. hololepidotus* ") in 5–7 m in Algoa Bay (Beckley, 1986) suggest that spawning occurs in less than 50 m depth of water. However, even though early life stages of larvae and juvenile recruits (see "nursery areas" below) are found just seaward of the surf zone (5–7 m), it is not certain whether spawning occurs in this area or whether it occurs in slightly deeper water and the eggs and larvae are transported shorewards by currents.

Although spawning in other sciaenids, including *A. japonicus*, occurs at night (Fish and Cummings, 1972; Takemura et al., 1978; Holt et al., 1985; Saucier and Baltz, 1993; Connaughton and Taylor, 1995; Griffiths, in press, b), the fact that large proportions of ripe and running females caught in seine nets in False Bay (Fig. 11) were caught between 11:30 h and 14:30 h, suggests that spawning in *A. inodorus* may occur during the day. The water temperature in which ripe and running females were captured was 18–19°C, but as indicated for other sciaenids (Saucier

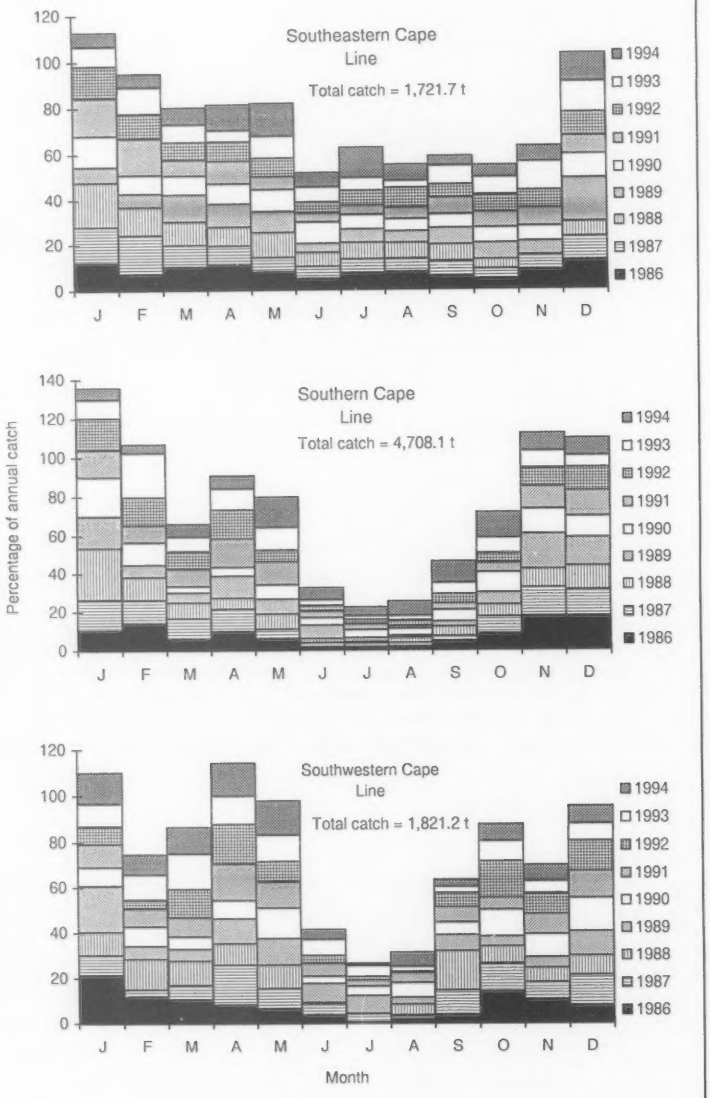


Figure 5

Cumulative monthly catches of *Argyrosomus inodorus* made by South African commercial linefishermen in each region, expressed as percentages of the respective annual catches, 1986–94.

and Baltz, 1993; Connaughton and Taylor, 1995), a range of spawning temperatures is expected. Hydrophonic monitoring of drumming levels (Takemura et al., 1978; Saucier and Baltz, 1993; Connaughton and Taylor, 1995) would provide better information on the times, sites, and oceanographic conditions necessary for spawning of silver kob.

Although the ovaries of *A. inodorus* were not examined microscopically, substantial increases in the number of spent gonads towards the end of, and immediately after, the five-month spawning season (Fig. 10), as opposed to throughout the season, suggest that they are multiple spawners. Unfortunately partially spawned fish could not be identified macro-

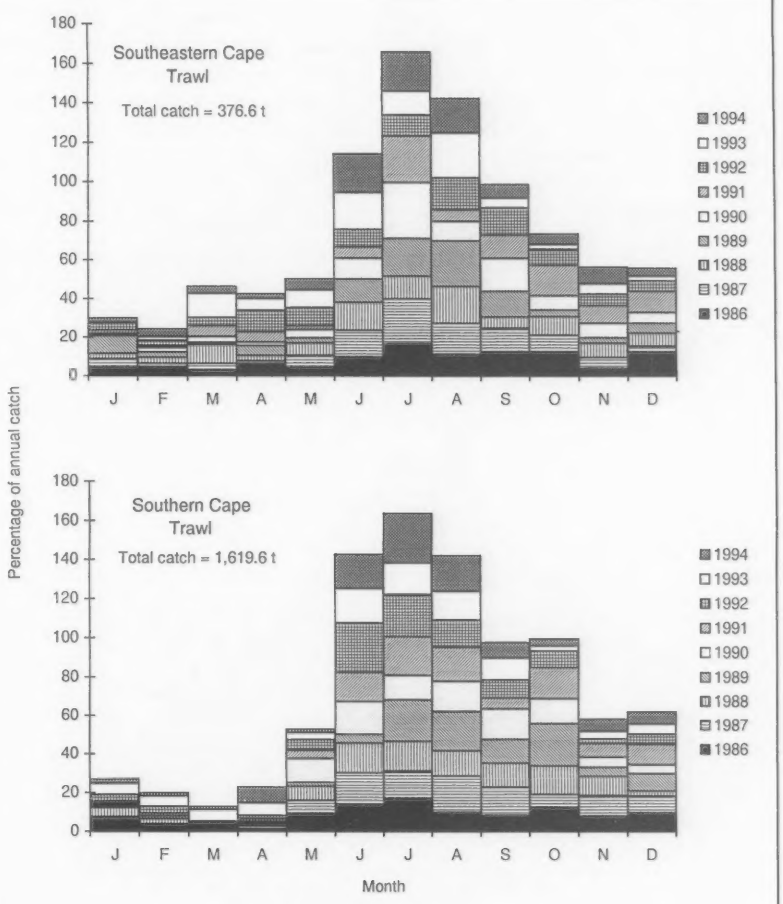


Figure 6

Cumulative monthly landings of *Argyrosomus inodorus* made by the inshore trawl fishery in the southeastern Cape and the southern Cape, expressed as percentages of the respective annual totals, 1986–94.

scopically. Multiple-batch spawning has been described for several other species of sciaenids, e.g. *Sciaenops ocellatus* (Fitzhugh et al., 1988), *Seriphus politus* (DeMartini and Fountain, 1981), *Cheilotrema saturnum* (Goldberg, 1981), *Genyonemus lineatus* (Love et al., 1984), *Cynoscion nebulosis* (Brown-Peterson et al., 1988), *Pogonias cromis* (Fitzhugh et al., 1993; Nieland and Wilson, 1993), and *Micropogonias undulatus* (Barbieri et al., 1994).

Sex ratios

From the total numbers of silver kob sampled, it was evident that there were significantly more females (1.6×) in the southeastern Cape, more males (1.2×) in the southern Cape, and more females (2.1×) in the southwestern Cape (Table 3). Except for the smallest size class sampled in the southeastern Cape (where males predominated), all other size classes sampled in the southeastern Cape and in the southwestern Cape contained significantly more females. Smale (1985) also recorded consistently higher proportions of female "*A. hololepidotus*" per 100-mm length class for fish sampled in the southeastern Cape (1978–81). Although he included both *A. inodorus* and *A. japonicus* in his study, the latter species recruits to the line fishery only at about 1,000 mm TL (Griffiths, in press, b), therefore his speci-

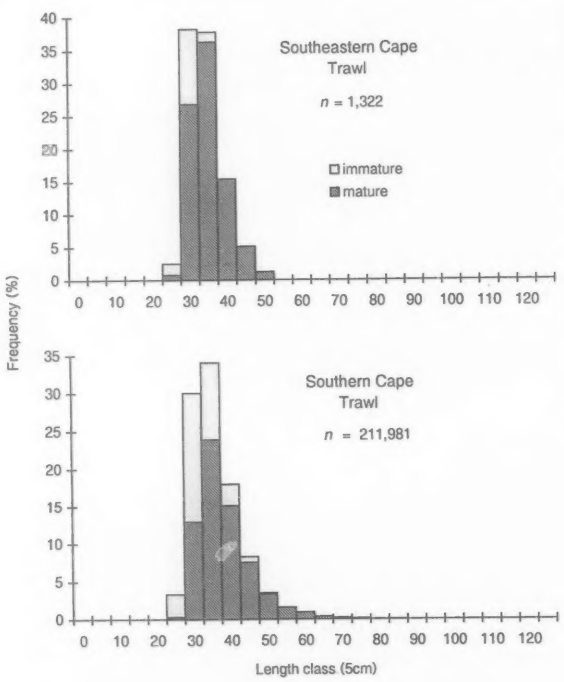


Figure 7

Total length distributions of *Argyrosomus inodorus* landed by the inshore trawl fishery in the southeastern Cape and in the southern Cape, 1990–94. The proportions of immature fish were based on regional averages of the values for males (drumming muscle method) and females presented in Figure 8.

Table 3

Sex ratios of *Argyrosomus inodorus* from three regions along the South African eastern seaboard. * = significant difference at $P<0.05$.

Total length (mm)	Southeastern Cape			Southern Cape			Southwestern Cape		
	M : F	*n*	χ^2	M : F	*n*	χ^2	M : F	*n*	χ^2
100–199	1.4 : 1	188	4.2*	1.2 : 1	114	0.9			
200–299	1 : 1.2	562	4.4*	1.1 : 1	320	1.3			
300–399	1 : 1.7	1,194	72.4*	1.2 : 1	289	2.5	1 : 1.3	72	0.9
400–499	1 : 2.0	541	61.9*	1.3 : 1	544	10.6*	1 : 3.1	49	12.8*
500–599	1 : 2.9	212	49.1*	1.5 : 1	212	9.1*	1 : 1.7	57	4.0*
600–699	1 : 2.0	119	7.1*	1 : 1.2	76	0.8	1 : 2.6	36	7.1*
700–799	1 : 1.8	58	4.4*	1 : 1.2	30	0.1	1 : 1.8	61	13.8*
800–899	1 : 1.5	56	2.6*	1.1 : 1	25	0.0	1 : 2.0	77	8.1*
900–999	1 : 3.2	25	6.8*	1.9 : 1	43	3.9*	1 : 2.8	57	12.8*
1000–1099	1 : 6.3	21	11.6*	1.3 : 1	80	1.0	1 : 2.6	29	5.8*
1100–1199	1 : 1.5	5	0.2	1 : 1.1	30	0.1			
All sizes	1 : 1.6	2,982	158.7*	1.2 : 1	1,764	20.1*	1 : 2.1	446	57.4*

mens below this length were mostly *A. inodorus*. Of the 11 size classes sampled in the southern Cape, eight contained more males and three contained more females (Table 3). However, the ratios of only three of these size classes (each with more males) were significantly different from the expected 1:1. Because more males were sampled within most size classes in the southern Cape, it would appear that there are more males than females in this region and that the lack of significance for several of the size classes could be due to limitations of the statistical test. The chi-square test is based on absolute differences (between observed and expected) and does not take into account sample size, e.g. although a ratio of 1.2:1

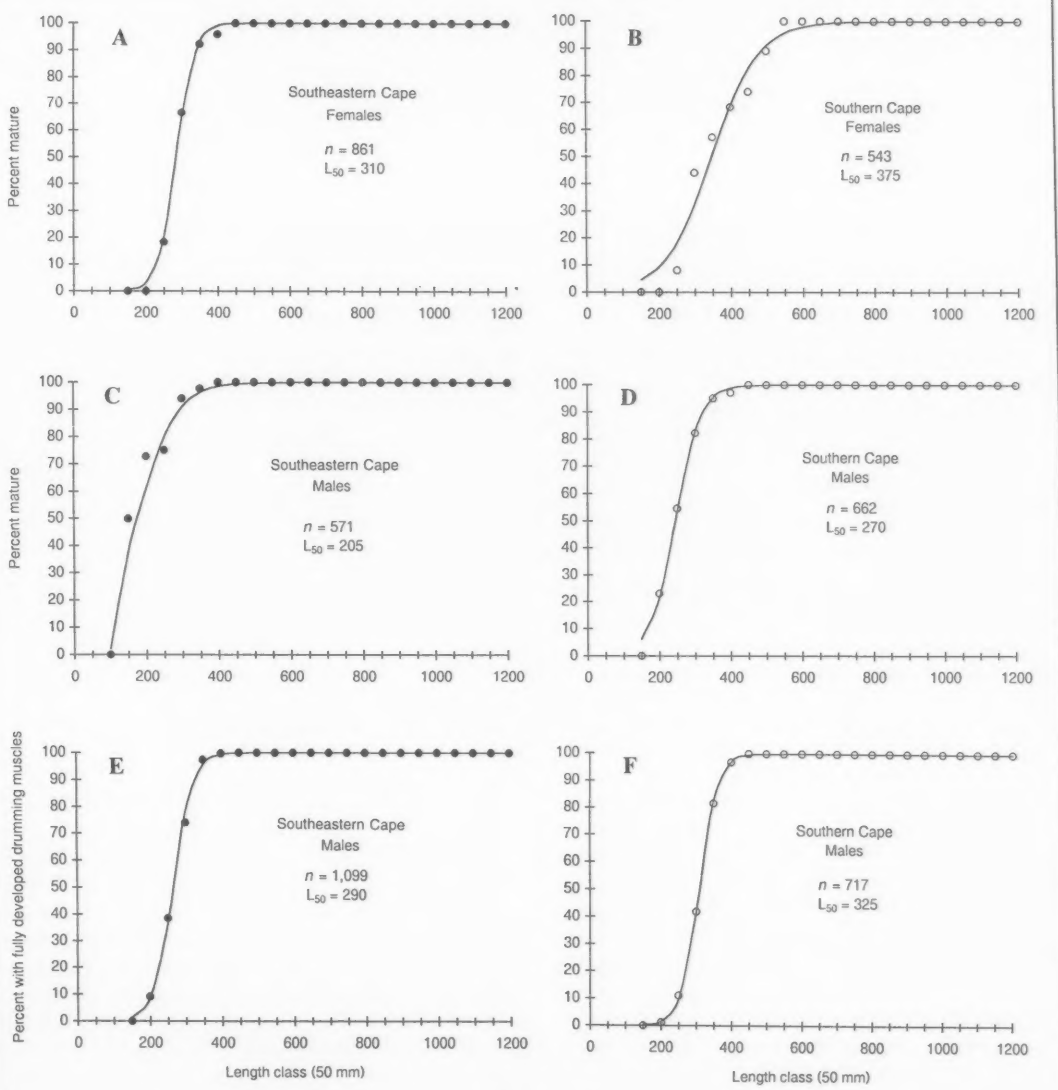


Figure 8

Percentage of mature female (gonad stage 3+) and male (gonad stage 3+ and drumming muscle stage 3) *Argyrosomus inodorus* by 50-mm total-length intervals, sampled during the spawning period in the southeastern Cape and in the southern Cape. The solid line describes the fitted logistical function. L_{50}= median length at first maturity (mm total length); n = sample size.

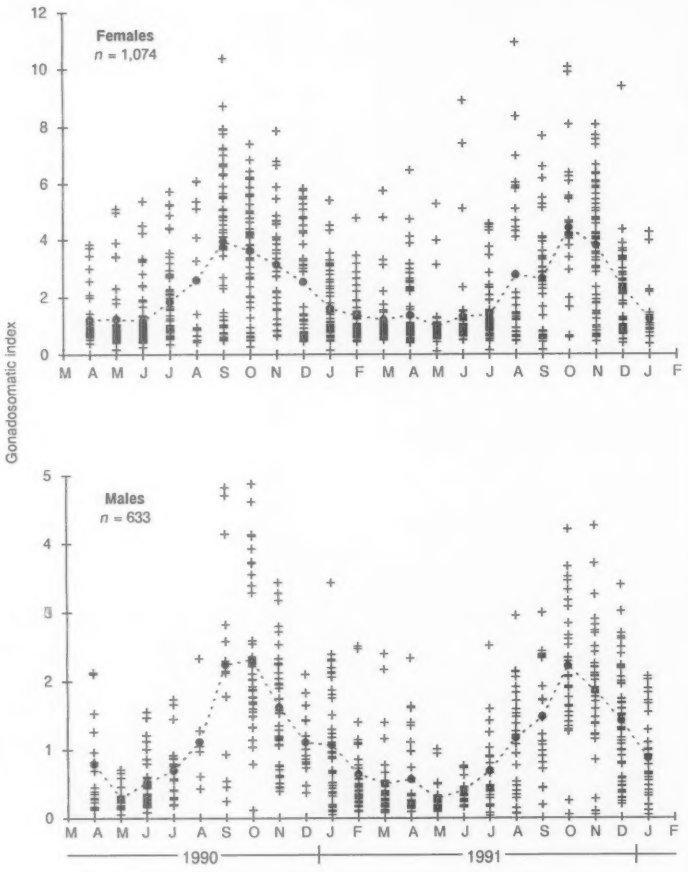


Figure 9

Mean monthly (circles) and monthly (crosses) gonadosomatic indices for mature female and male *Argyrosomus inodorus* sampled in the southeastern Cape, April 1990–January 1992. *n*=sample size.

(*n*=1,764) was significant (even at $P<0.001$), one of 1.3:1 (*n*=80) was not (Table 3). Thus researchers studying sex ratios should make every effort to obtain large samples, particularly if the chi-square method is to be used as a test for significant difference.

Nursery areas

Argysomus inodorus landed by the line fishery were mostly adult fish between 40 and 120 cm TL (Fig. 12). Although fish <40 cm TL were not represented in the present study owing to the minimum size limit imposed on linefishermen, experimental linefishing indicated that silver kob on the linefishing grounds (reef substrata) were mostly >30 cm TL (Fig. 12) and that in the southeastern Cape and in the southern Cape they were generally larger than the female L_{50} estimates.

Argysomus inodorus trawled between Cape Agulhas and Port Alfred during SCBS's (nonreef substrata) ranged between 5 and 120 cm TL but were generally <45 cm TL, and largely immature (Fig. 13). The modal length class increased from 20–25 cm at depths of 25–50 m, to 25–30 cm at 50–100 m and 30–35 cm at 100–150 m; and the proportion of mature fish increased accordingly. Although depths <25 m were not sampled during SCBS's, silver kob (identified as "*A. hololepidotus*") trawled in <9 m during an earlier survey of the bays between Mossel Bay and Algoa Bay were mostly 9–18 cm TL (Smale, 1984). Beckley (1984) recorded *A. inodorus* (also iden-

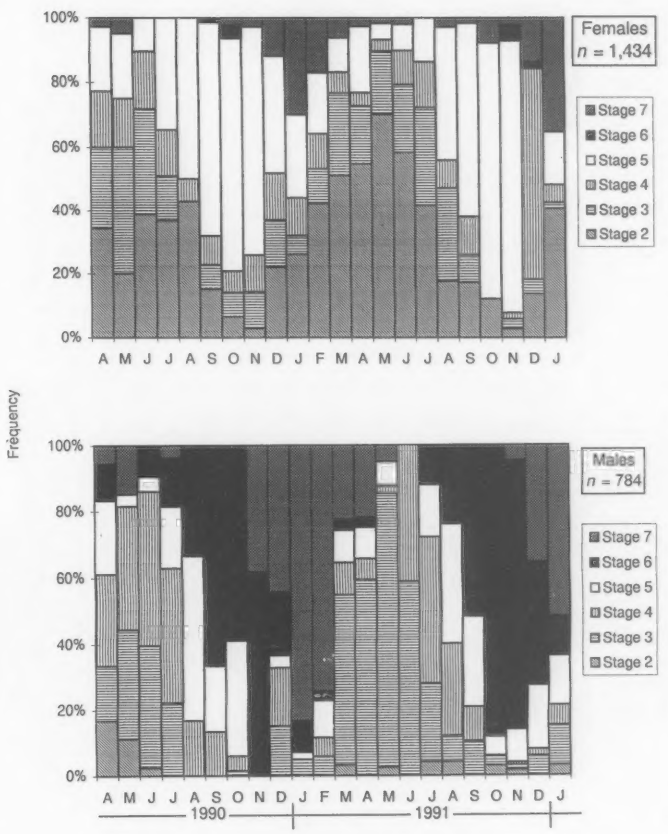


Figure 10

Monthly percentage of gonad stages for mature female and male *Argyrosomus inodorus* in the southeastern Cape, April 1990–January 1992. *n*=sample size.

tified as "*A. hololepidotus*") as small as 1.3 cm TL just behind the breakers (5–7 m depth) in Algoa Bay. Voucher specimens (including otoliths) from both of these studies were identified as *A. inodorus*. There is therefore a trend of increasing length with increasing depth and distance from the shore for juvenile silver kob occurring between Cape Agulhas and Port Alfred. This finding suggests that juveniles are recruited to the nursery grounds just seaward of the surf zone and that they move farther offshore as they grow. Silver kob do not enter estuaries, and between Cape Agulhas and the Kei River, they do not occur in the surf zone (Griffiths and Heemstra, 1995). The SCBS CPUE-analyses revealed that juvenile *A. inodorus* were not homogenously distributed over the survey area but were found mostly in <120 m depth and comprised two disjunct distributional ranges, i.e. Cape Agulhas to Mossel Bay and Cape St Francis to Port Alfred (Fig. 3). Although the inshore areas of the southwestern Cape are not suitable for trawling, analysis of commercial beach-seine catches (Lamberth et al., 1994) revealed that juvenile *A. inodorus* (identified as "*A. hololepidotus*") are also found in False Bay.

Discussion

The results of this study strongly suggest that silver kob between Cape Point and the Kei River comprise three discrete stocks. The foci of each of these stocks are False Bay in the southwestern Cape, Stil Bay in the southern Cape, and Port Alfred in the southeastern Cape. Tagging evidence indicates that there is lim-

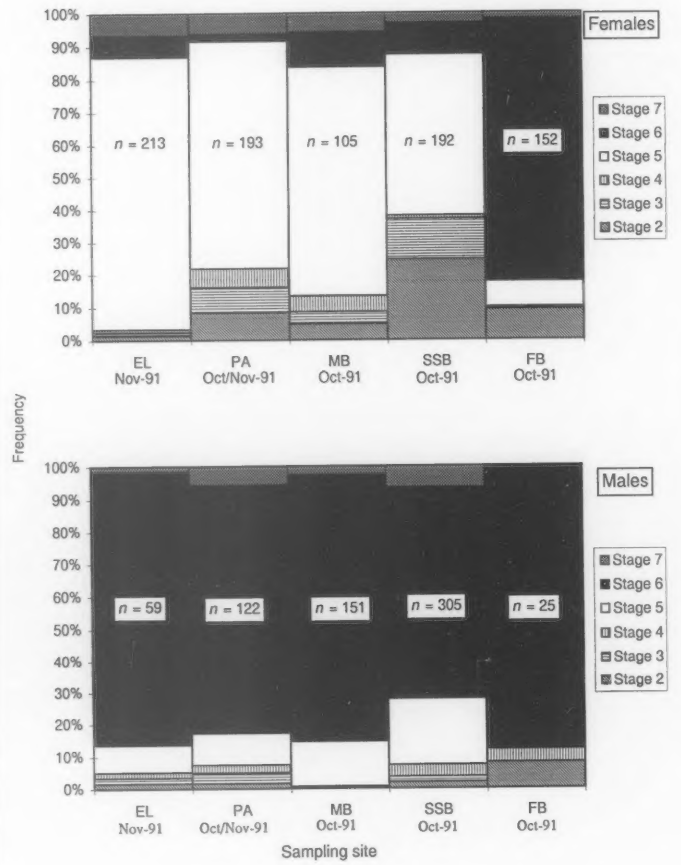


Figure 11

Percentage of gonad stages observed for male and female *Argyrosomus inodorus* at five localities during the peak spawning season in 1991. EL=East London, PA=Port Alfred, MB=Mossel Bay, SSB= St Sebastian Bay, FB=False Bay, and *n*=sample size. Fish sampled at the first four localities were caught by hook and line, whereas those in False Bay were caught with beach-seine nets.

ited exchange between the southwestern Cape and the southern Cape stocks but that there is no exchange between either of these two stocks and the one in the southeastern Cape. Analysis of catch and tagging data shows that each of the three stocks is concentrated inshore in summer but disperses seawards in winter.

The distribution of silver kob on the South African eastern seaboard, including the existence of the three stocks and their onshore–offshore movement, is also supported by regional oceanographic patterns. During spring, summer, and autumn, the east coast between Cape Agulhas and the Kei River is characterized by three zones: 1) a warm inshore band (0–20 m) with an average temperature of 21°C (although in certain areas temperatures can drop to <12°C for brief periods following coastal upwelling); 2) a zone of intermediate temperature (12–19°C) between 20 and 50 m; and 3) a bottom mixed layer of <12°C found below 50 m (Eagle and Orren, 1985; Swart and Largier, 1987; Goschen and Schumann, 1988; Boyd and Shillington, 1994; Greenwood and Taunton-Clark[2]). Silver kob prefer temperatures of 13–16°C (Fig. 14) and are therefore mainly confined to the

[2] Greenwood, C., and J. Taunton-Clark. 1992. An atlas of mean monthly and yearly average sea surface temperatures around the southern African coast. Sea Fisheries Research Institute, Private Bag X2, Roggebaai 8012, Cape Town, South Africa. Internal report 124, 112 p.

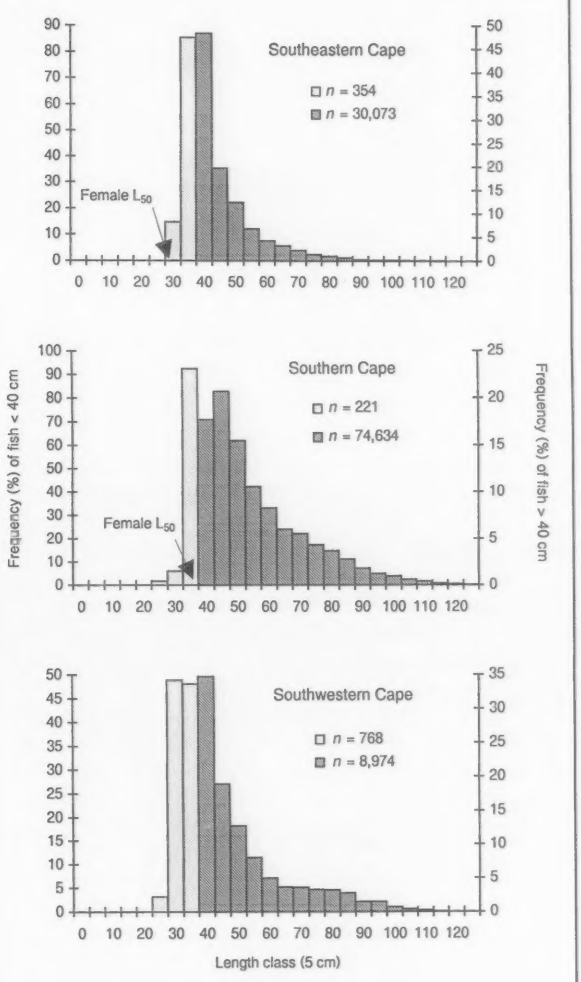


Figure 12

Regional total-length distributions of *Argyrosomus inodorus* 1) landed by the South African line fishery, 1990–94 (hatched lines) and 2) caught on linefish grounds during experimental fishing operations and which were below the minimum size limit (40 cm) (shaded area). Arrows indicate female median length at maturity (L_{50}). L_{50} was not estimated for the southwestern Cape.

intermediate zone. During spring, summer, and autumn, the intermediate zone is restricted to an area within a few kilometres of the coast and is within easy range of line boats (see 50-m isobath in Fig. 1). In winter the bottom mixed layer retreats down the shelf to about 100 m (Schumann and Beekman, 1984; Eagle and Orren, 1985; Swart and Largier, 1987). As the intermediate zone expands, I propose that *A. inodorus* stocks disperse seaward, moving beyond the grounds of the linefishery and onto the inshore trawling grounds. Because Agulhas Bank is much narrower in the southeastern Cape than in the southern Cape (Fig. 1), offshore movement would have been more constrained than in the latter region and hence would explain the higher winter line catches in the southeastern Cape (Fig. 5).

Owing to a higher degree of coastal upwelling off the southwestern Cape, the bottom mixed layer

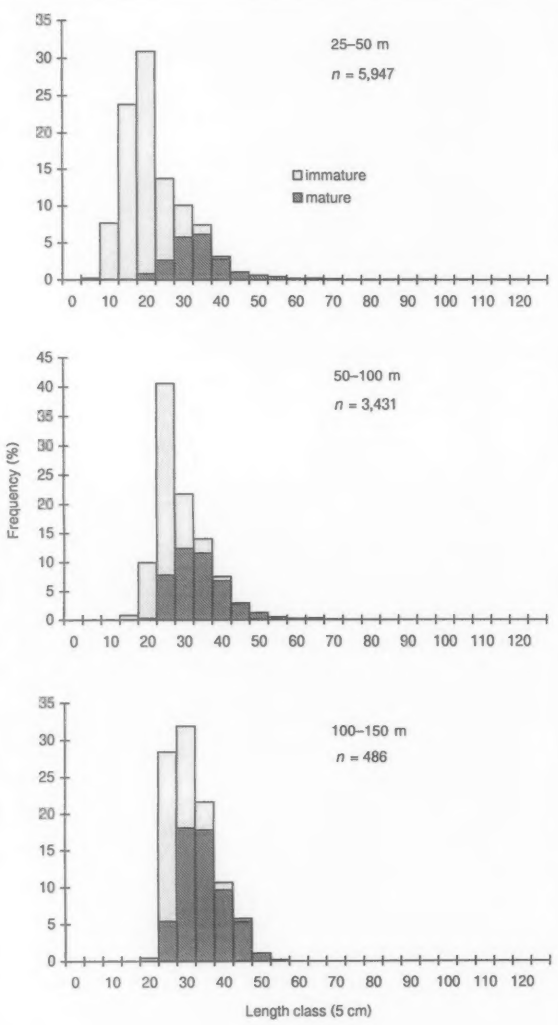


Figure 13

Total-length distributions per depth range for *Argyrosomus inodorus* trawled between Cape Agulhas and Port Alfred during South Coast Biomass Cruises, 1990–94. The proportion of immature fish in each length class is an average of the values presented for males (drumming muscle method) and females in the southeastern Cape and the southern Cape in Figure 8.

(<12°C) is shallower (20 vs. 50 m on the east coast) from spring to autumn, and the temperatures above 20 m are generally 13–19°C during this period (Atkins, 1970; Boyd et al., 1985; Largier et al., 1992; Greenwood and Taunton-Clark[2]). Because inshore temperatures are lower than those on the east coast, silver kob are caught by linefishermen from the surf zone to depths of 20 m. As along the east coast, the bottom mixed layer deepens to about 100 m in winter (Atkins, 1970; Boyd et al., 1985; Largier et al., 1992), and silver kob are expected to move offshore (as indicated by catch trends [Fig. 5]). Because the depth contours broaden east of Cape Hangklip, it is possible that there is also an easterly component to the offshore dispersal of silver kob. A seaward and eastward winter migration has also been postulated

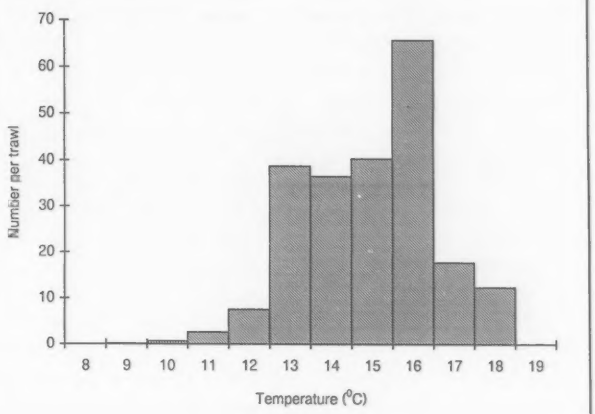


Figure 14

Mean number of *Argyrosomus inodorus* per trawl for each 1°C bottom temperature category during South Coast Biomass Surveys, 1987–95.

for subadult *Atractoscion aequidens* (Sciaenidae), occurring in the southwestern Cape (Griffiths and Hecht, 1995a).

Data from all 14 SCBS's revealed that the bottom mixed layer (<12°C) extends farther up the shelf (and is closer to the coast) in the area between Knysna and Cape St Francis (Fig. 15; see also Le Clus and Roberts, 1995), thus inhibiting exchange between the silver kob stock in the southern Cape and that in the southeastern Cape. Along the eastern and western sides of False Bay, the 20-m isobath is found <500 m from the shore (van Ballegooyen, 1991). Because suitable temperatures for silver kob are found at depths shallower than 20 m in the southwestern Cape during spring to autumn, the movement of silver kob into or out of False Bay (the focus of the southwestern Cape stock) during this period is therefore restricted. In addition, the upwelled bottom mixed layer frequently extends to the shore between Cape Hangklip and Cape Agulhas, particularly from December to April (Boyd et al., 1985; Largier et al., 1992), thus further limiting exchange between in False Bay and in the southern Cape.

Spawning occurred throughout the distributional ranges of all three stocks and peaked in spring (Sept–Nov) in all regions. Sizes and ages at maturity were, however, substantially smaller in the southeastern Cape than in the southern Cape. Female L_{50} was 310 mm TL (1.3 yr) in the former and 375 mm TL (2.4 yr) in the latter region. Changes in ages and sizes at maturity have been correlated with exploitation rate for several fish species (Healey, 1975; Borisov, 1978; Ricker, 1981; Beacham, 1983; Wysokinski 1984; Armstrong et al., 1989). Because fishing mortality is significantly higher in the southeastern Cape than in the southern Cape (F=0.67 vs. 0.42)(Griffiths, in press, c), the smaller sizes at maturity recorded for the southeastern Cape are possibly due to fishing pressure. The mechanisms accounting for the decreases in the size and age at maturity in the southeastern Cape, however, remain to be identified. One explanation is that the younger ages and smaller sizes at maturity for silver kob in the southeastern Cape could be the result of density-dependent effects; higher mortality results in more food for surviving fish, in additional energy for gonad growth, and consequently in earlier maturity. In several other species, ages or sizes (or both) at maturity have been correlated with the amount of accumulated surplus energy within a fish (Armstrong et al., 1989; Rowe et al., 1991; Berglund, 1992; Kerstan[3]). On the other hand, Ricker (1981) stated that "If a fish matures before it is large enough to be vulnerable to fishing, its expectation of contributing to future generations will be greater than that of a sibling of the same size that does not mature until a year later. The result can be a gradual decrease in the mean size at maturity." Female silver kob attain the minimum size limit for the line fishery (400 mm TL) at ca. 2.8 yr in both the southeastern Cape and the southern Cape (Griffiths, in press, a). Approximately 95% of these

[3] Kerstan, M. 1995. Sex ratios and maturation patterns of horse mackerel (*Trachurus trachurus*) from the NE-and SE-Atlantic and the Indian Ocean—a comparison. ICES council meeting H:6, 20 p. (Mimeo.)

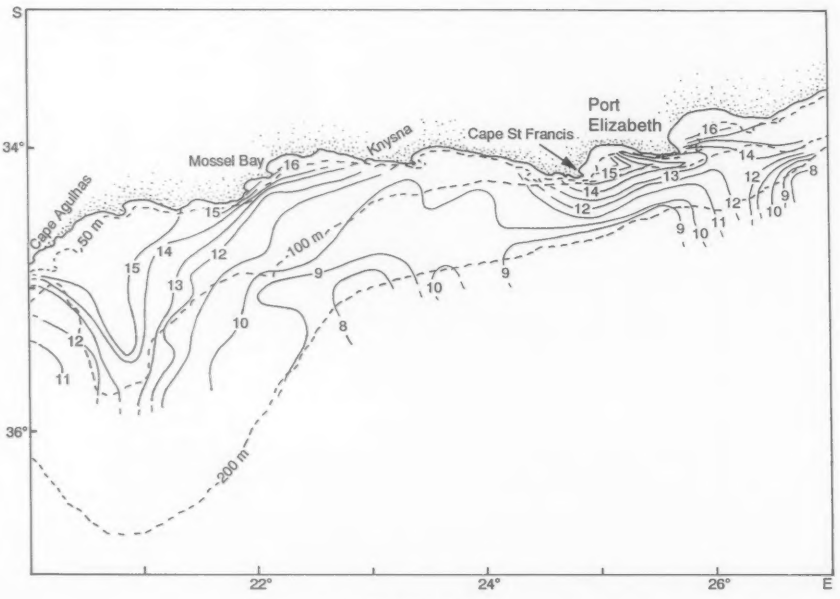


Figure 15

Bottom temperature structure on the central and eastern Agulhas Bank during the October 1987 South Coast Biomass Survey. This temperature pattern, with cold water (<12°C) at shallower depths and closer to the coast between Knysna and Cape St Francis, was typical of SCBS's between 1987 and 1995. See Figure 1 for additional localities.

new recruits are mature in the southeastern Cape, but only 69% in the southern Cape. Assuming that size at maturity for silver kob in the southeastern Cape was at one time similar to that in the southern Cape, the removal of late-maturing fish, before they had spawned for the first time, could have reduced the sizes and ages at maturity to those recorded in this study. The large contribution of recruits (400–450 mm TL) to the southeastern Cape line catch (ca. 50% by number)(Fig. 12), supports this hypothesis.

Investigation of sex ratios showed that there are substantially more females in the southeastern Cape (1.6×) and southwestern Cape (2.1×) stocks, but more males in the southern Cape (1.2×). Most natural populations tend to stabilize at sex ratios of 1:1 (Conover and Van Voorhees, 1990), including those of other sciaenids (Shepherd and Grimes, 1984; Murphy and Taylor, 1989; Wilson and Nieland, 1994; Ross et al., 1995; Griffiths and Hecht, 1995a). The deviations from this ratio observed for South African silver kob are not easily explained. Basically, the reasons for an observed sex ratio that deviates from unity may be grouped into three categories: 1) more individuals of either sex are produced (e.g. environmental sex determination); 2) equal numbers of both sexes are produced, but those of one sex are diminished through either emigration or mortality; and 3) sampling methods are biased towards one of the sexes. Although environmental sex determination can temporarily result in skewed sex ratios in some species (Conover and Heins, 1987), frequency-dependent selection is expected to return the ratios of such populations to equality through future generations (Conover and Van Voorhees, 1990). Higher proportions of either sex over most size classes (therefore spanning several age classes) in each region, with consistency over two periods (1978–81 and 1990–91) in the southeastern Cape, render environmental sex determination an unlikely cause of the observed sex ratios. Male emigration from the southeastern Cape and the southwestern Cape to the southern Cape is also unlikely. Because the smallest size class sampled in the southeastern Cape consisted of males without drumming muscles and also consisted of more males than females, it is tempting to suggest that male drumming during the protracted spawning season may have resulted in sex-selective predation in this region and in the southwestern Cape. However, there is no reason to believe that predation rates should be higher in the southeastern Cape and the south-

western Cape than in the southern Cape. Because capture methods were the same in all three regions, increased vulnerability of either sex to capture is not a plausible explanation either. Thus additional research is required before the regionally specific sex ratios observed for *A. inodorus* can be adequately explained.

Silver kob use inshore (<120 m depth) sand and mud substrata as nursery areas. They apparently recruit (ca.1.5 cm TL) just seawards of the surf zone (5–7 m depth) but move offshore with growth. Upon attaining maturity they recruit to adult populations that are found on reefs. Distributional analyses have revealed that juvenile *A. inodorus* between Cape Agulhas and the Kei River comprise two disjunct distributional ranges, one in the southern Cape and the other in the southeastern Cape. Although the inshore areas of the southwestern Cape are not suitable for trawling, analysis of commercial beach-seine catches (Lamberth et al., 1994) has revealed that juvenile *A. inodorus* (identified as "*A. hololepidotus*") are also found in False Bay. The existence of nursery areas and spawning grounds in each of the three sampling regions, and the differences in size at maturity and sex ratio, lend further credence to the separate stock concept.

Conclusion

Distributional analyses based on fishery dependant and fishery independent data revealed that there are three areas of silver kob abundance between Cape Point and the Kei River. The fact that each of these "populations" has its own spawning grounds and nursery areas and the fact that there are observed differences in growth rates, otolith-dimension and fish-length relationships, growth zone structure, sizes at maturity, and sex ratios, together indicate that these "populations" represent separate stocks. This three-stock concept is further supported by migratory patterns indicated from catch and tagging data and by the oceanography between Cape Point and the Kei River.

Although genetic differentiation should ideally form the basis of inferences concerning stock distinction, analyses based on protein electrophoresis and mitochondrial DNA have generally been unsuccessful in differentiating between marine stocks (see Campana and Casselman, 1992; Pawson and Jennings, 1996), including those of sciaenids (Ramsey and Wakeman, 1987; Graves et al., 1992; King and Pate, 1992). Although none of the data used to infer separate silver kob stocks necessarily reflect genetic differences (Ihssen et al., 1981), the identification of three allopatric units of fish with different population parameters indicates that each may respond differently to fishing and that the exploitation of one unit will not affect the size or composition of the other two, thereby supporting separate management of the three units and their stock status (Spangler et al., 1981; Brown and Darcy, 1987; Campana and Gagné, 1995; Edmonds et al., 1995; Pawson and Jennings, 1996).

Recent application of per-recruit models to South African silver kob (based on the results presented in this study) indicates that, owing to their different population parameters, each stock requires a different combination of fishing mortality and age at first capture for optimal exploitation (Griffiths, in press, c). Therefore *A. inodorus* should ideally be managed on a regional and not on a national basis. Studies of the life histories of two other South African sciaenids, *Atractoscion aequidens* (Griffiths and Hecht, 1995a) and *Argyrosomus japonicus* (Griffiths and Hecht, 1995b; Griffiths, in press, b), have revealed that they consist of single stocks with allopatric age or size-determined subpopulations, even though they occur from Cape Point to southern Mozambique and are therefore more widely distributed on the eastern seaboard than are *A. inodorus*. Inferences from stock structure, based on closely related taxa, are therefore not desirable because they could result in erroneous conclusions and consequently in poor management.

Acknowledgments

The author thanks Chris Wilke, Peter Sims, and John Prinsloo (Sea Fisheries Research Institute) for providing CPUE and length-frequency summaries for the line fishery, the inshore trawl fishery, and South Coast Biomass Surveys, respectively; M. Roberts, A. Boyd, and G. Nelson for oceanographic data and for helpful discussions on the oceanography of the study area; Malcolm Smale and Larry Hutchings for valuable comments on an earlier draft of the manuscript; and all those commercial and recreational fishermen who made their catches available for sampling. The project was partially funded by the Sea Fisheries Fund.

Literature cited

Armstrong, M. J., B. A. Roel, and R. M. Prosch.
1989. Long-term trends in patterns of maturity in the southern Benguela pilchard population: evidence for density-dependance? S. Afr. J. Mar. Sci. 8:91–101.

Atkins, G. R.
1970. Thermal structure and salinity of False Bay. Trans. R. Soc. S. Afr. 39:117–128.

Badenhorst, A., and M. J. Smale.
1991. The distribution and abundance of seven commercial trawl fish from the Cape south coast of South Africa, 1986–1990. S. Afr. J. Mar. Sci. 11:377–393.

Barbieri, L. R., M. E. Chittenden Jr., and S. K. Lowerre-Barbieri.
1994. Maturity, spawning, and ovarian cycle of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. Fish. Bull. 92:671–685.

Beacham, T. D.
1983. Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian shelf in the northwest Atlantic ocean. Fish. Bull. 81:303–321.

Beckley, L. E.
1984. Shallow water trawling off the Swartkops estuary, Algoa Bay. S. Afr. J. Zool. 19:248–250.
1986. The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish. S. Afr. J. Zool. 21:244–252.
1993. Linefish larvae and the Agulhas Current. *In* L. E. Beckley and R. P. van der Elst (eds.), Fish, fishers and fisheries: proceedings of the second South African marine linefish symposium, p. 57–63. Oceanographic Res. Inst., Special Publ. 2.

Berglund, I.
1992. Growth and early sexual maturation in Baltic salmon (*Salmo salar*) parr. Can. J. Zool. 70:205–211.

Borisov, V. M.
1978. The selective effect of fishing on the population structure of species with a long life cycle. J. Ichthyol. 18:896–904.

Boyd, A. J., and F. A. Shillington.
1994. Physical forcing and circulation patterns on the Agulhas Bank. S. Afr. J. Mar. Sci. 90: 114–122.

Boyd, A. J., B. B. S. Tromp, and D. A. Horstman.
1985. The hydrology off the South African south-western coast between Cape Point and Danger Point in 1975. S. Afr. J. Mar. Sci. 3:145–168.

Brown, B. E., and G. H. Darcy.
1987. Stock assessment/stock identification: an interactive process. *In* Proceedings of the stock indentification workshop, p. 1–23. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC 199.

Brown-Peterson, N., P. Thomas, and C. R. Arnold.
1988. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in South Texas. Fish. Bull. 86:373–388.

Campana, S. E., and J. M. Casselman.
1992. Stock discription using otolith shape analysis. Can. J. Fish. Aquat. Sci. 50: 1062–1083.

Campana, S. E., and J. A. Gagné.
1995. Cod stock discrimination using ICPMS elemental essays of otoliths. *In* D. H. Secor, J. M. Dean, and S. E. Campana (eds.), Recent developments in fish otolith research, p 671–691. Univ. South Carolina Press, Columbia, SC.

Connaughton, M. A.
1996. Drumming, courtship, and spawning behaviour in captive weakfish, *Cynoscion regalis*. Copeia 1996:195–199.

Connaughton, M. A., and M. H. Taylor.
1995. Seasonal and daily cycles in sound production associated with spawning in the weakfish, *Cynoscion regalis*. Env. Biol. Fish. 42:233–240.

Conover, D. O., and S. W. Heins.
1987. Adaptive variation in environmental and genetic sex determination in a fish. Nature (Lond.) 326:496–498.

Conover, D. O., and D. A. Van Voorhees.
1990. Evolution of a balanced sex ratio by frequency-dependent selection in a fish. Science (Wash. D.C.):1556–1557.

DeMartini, E. E., and R. K. Fountain.
1981. Ovarian cycling frequency and batch fecundity of the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull. 79:547–560.

Eagle, G. A., and M. J. Orren.
1985. A seasonal investigation of the nutrients and dissolved oxygen in the water column along two lines of stations south and west of South Africa. Rep. S. Afr. Counc. Sci.. Ind. Res. 567, 52 p. + 7 tables + 119 figures.

Edmonds, J. S., S. Caputi, M. J. Moran, W. J. Fletcher, and M. Morita.
1995. Population discrimination by variation in concentrations of minor and trace elements in sagittae of two Western Australian teleosts. *In* D. H. Secor, J. M. Dean, and S. E. Campana (eds.), Recent developments in fish otolith research, p. 617–627. Univ. South Carolina Press, Columbia, SC.

Ferriera, T. A.
1993. recreational anglers view of marine linefish management. *In* L. E. Beckley and R. P. van der Elst (eds.), Fish, fishers and fisheries: proceedings of the second South African marine linefish symposium, p. 182–185. Oceanographic Res. Inst., Special Publ. 2.

Fish, M. P., and W. C. Cummings.
1972. A 50-dB increase in sustained ambient noise from fish (*Cynoscion xanthulus*). J. Acoust. Soc. Am. 52:1266–1270.

Fitzhugh, C. R., T. G. Snider III, and B. A. Thompson.
1988. Measurement of ovarian development in red drum (*Sciaenops ocellatus*) from offshore stocks. Contrib. Mar. Sci., Suppl. to vol. 30:79–83.

Fitzhugh, C. R., B. A. Thompson, and T. G. Snider III.
1993. Ovarian development, fecundity, and spawning frequency of black drum *Pogonias cromis* in Louisiana. Fish. Bull. 91:244–253.

Goldberg, S. R.
1981. Seasonal spawning cycle of the black croaker, *Cheilotrema saturnum* (Sciaenidae). Fish. Bull. 79: 561–562.

Goschen, W. S., and E. H. Schumann.
1988. Ocean current temperature structures in Algoa Bay and beyond in November 1986. S. Afr. J. Mar. Sci. 7:101–116.

Graves, J .E., J. R. Mcdowell, and L. M. Jones.
1992. A genetic analysis of weakfish *Cynoscion regalis* stock structure along the mid-Atlantic coast. Fish. Bull. 90:469–475.

Griffiths, M. H.
In press, a. Age and growth of South African silver kob, *Argyrosomus inodorus* (Sciaenidae), with evidence for separate stocks, based on otoliths. S. Afr. J. Mar. Sci. 17.
In press, b. On the life-history of *Argyrosomus japonicus* (Sciaenidae) off the east coast of South Africa. S. Afr. J. Mar. Sci. 17.
In press, c. The application of per-recruit models to *Argyrosomus inodorus*, an important South African sciaenid fish. Fish. Res.

Griffiths, M. H., and T. Hecht.
1995a. On the life-history of *Atractoscion aequidens*, a migratory sciaenid off the east coast of southern Africa. J. Fish Biol. 47:962-985.
1995b. Age and growth of South African dusky kob, *Argyrosomus japonicus* (Sciaendae), based on otoliths. S. Afr. J. Mar. Sci. 16:119–128.

Griffiths, M. H., and P. C. Heemstra.
1995. A contribution to the taxonomy of the marine fish genus *Argyrosomus* (Perciformes: Sciaenidae) with descriptions of two new species from southern Africa. Ichthyol. Bull., J.L.B. Smith. Inst. Ichthyol. 65, 40 p.

Healey, M. C.
1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. 32:427–448.

Hecht, T., and R. L. Tilney.
1989. The Port Alfred fishery: a description and preliminary evaluation of a commercial linefishery on the South African east coast. S. Afr. J. Mar. Sci. 8:103–117.

Holt, G. J., S. A. Holt, and C. R. Arnold.
1985. Diel periodicity of spawning in sciaenids. Mar. Ecol. Prog. Ser. 27:1–7.

Ihssen, P. E., H. E. Booke, J. M. Casselman, J. M. Mcglade, N. R. Payne, and F. M. Utter.
1981. Stock identification: materials and methods. Can. J. Fish. Aquat. Sci. 38:1838–1855.

Japp, D. W., P. Sims, and M. J. Smale.
1994. A review of fish resources on the Agulhas Bank. S. Afr. J. Sci. 90:123–134.

King, T. L., and H. O. Pate.
1992. Population structure of spotted seatrout inahabiting the Texas Gulf coast: allozyme perspective. Trans. Am. Fish. Soc. 121:746–756.

Lamberth, S. J., B. A. Bennett, and B. M. Clark.
1994. Catch composition of the commercial beach-seine fishery in False Bay, South Africa. S. Afr. J. Mar. Sci. 14:69–78.

Largier, J. L., P. Chapman, W. T. Peterson, and V. P. Swart.
1992. The western Agulhas Bank: circulation, stratification and ecology. *In* A. I. L. Payne, K.H. Brink, K. H. Mann, and R. H. Hilborn (eds.), Benguela trophic functioning, p. 319–339. S. Afr. J. Mar. Sci. 12.

Le Clus, F., and M. J. Roberts.
1995. Topographic and hydrographic effects on catch rates of *Austroglossus pectoralis* (Soleidae) on the Agulhas Bank. S. Afr. J. Mar. Sci. 16:321–332.

Love, M. S., G. E. McGowen, W. Westphal, R. J. Lavenberg, and L. Martin.
1984. Aspects of the life history and fishery of the white croaker, *Genyonemus lineatus* (Sciaenidae), off California. Fish. Bull. 82:179–198.

Murphy, M. D., and R. G. Taylor.
1989. Reproduction and growth of black drum, *Pogonias cromis*, in northeast Florida. Northeast Gulf Sci. 10: 127–137.

Nieland, D. L., and C. A. Wilson.
1993. Reproductive biology and annual variation of reproductive variables of black drum in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 122:318–327.

Pawson, M. G., and S. Jennings.
1996. A critique of methods for stock identification in marine capture fisheries. Fish. Res. 25:203–217.

Ramsey, P. R., and J. M. Wakeman.
1987. Population structure of *Sciaenops ocellatus* and *Cynoscion nebulosis* (Pisces: Sciaenidae): biochemical variation, genetic subdivision and dispersal. Copeia 1987: 682–695.

Ricker, W. E.
1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38:1636–1656.

Ross, J. L., T. M. Stevens, and D. S. Vaughan.
1995. Age, growth, mortality and reproductive biology of red drums in North Carolina waters. Trans. Am. Fish. Soc. 124:37–54.

Rowe, D. K., J. E., Thorpe, and A. M. Shanks.
1991. Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Can. J. Fish. Aquat. Sci. 48:405–413.

Saucier, M. H., and D. M. Blatz.
1993. Spawning site selection by spotted seatrout, *Cynoscion nebulosus*, and black drum *Pogonias cromis*, in Lousiana. Env. Biol. Fish. 36:257–272.

Schumann, E. H., and L. J. Beekman.
1984. Ocean temperature structures on the Agulhas Bank. Trans. R. Soc. S. Afr. 45:191–203.

Shepherd, G. R., and C. B. Grimes.
1984. Reproduction of the weakfish, *Cynoscion regalis*, in the New York Bight and evidence for geographically specific life history characters. Fish. Bull. 82:501–511.

Smale, M. J.
1984. Inshore small-mesh trawling survey of the Cape south coast. Part 3. The occurrence and feeding of *Argyrosomus hololepidotus, Pomatomus saltatrix* and *Merluccius capensis.* S. Afr. J. Zool. 19:170–179.
1985. Aspects of the biology of *Argyrosomus hololepidotus* and *Atractoscion aequidens* (Osteichthyes: Sciaenidae) in the waters of the south-eastern Cape, South Africa. S. Afr. J. Mar. Sci. 3:63–75.

Spangler, G. R., A. H. Berst, and J. F. Koonce.
1981. Perspectives and policey recommendations on the relevance of the stock concept to fishery management. Can. J. Fish. Aquat. Sci. 38:1908–1914.

Swart, V. P., and J. L. Largier.
1987. Thermal structure of Agulhas Bank water. *In* A. I. L Payne., J. A. Gulland, and K. H. Brink (eds.), The Benguela and comparable ecosystems. S. Afr. J. Mar. Sci. 5: 243–253.

Takemura, A., T. Takita, and K. Mizue.
1978. Studies on the underwater sound—VII. Underwater calls of the Japanese marine drum fishes (Sciaenidae). Bull. Jpn. Soc. Fish. 44:121–125.

Van Ballegooyen, R. C.
1991. The dynamics relevant to the modelling of synoptic scale circulations within False Bay. Trans. R. Soc. S. Afr. 47:419–431.

Wilson, C. A., and D. L. Nieland.
1994. Reproductive biology of red drum, *Sciaenops ocellatus*, from the neritic waters of the northern Gulf of Mexico. Fish. Bull. 92:841–850.

Wysokinski, A.
1984. Length structure of the Cape horse mackerel population and changes in sexual maturity length in the Namibian region. Colln. Scient. Pap. Int. Comm. SE. Atl. Fish 11:91–98.

Estimates of tag-reporting and tag-shedding rates in a large-scale tuna tagging experiment in the western tropical Pacific Ocean

John Hampton
South Pacific Commission
B.P. D5 Noumea Cedex, New Caledonia
E-mail address: wjh@spc.org.nc

Abstract.—Estimates of tag-shedding and tag-reporting rates are required for an estimation of fishing and natural mortality rates from tagging data. For this purpose, double-tagging and tag-seeding experiments were undertaken by the South Pacific Commission, in conjunction with a large-scale tuna tagging program, in the western tropical Pacific Ocean during 1989–1992. Estimates of tag-shedding rates indicated that 89% (95% confidence interval of 82%–94%) of tagged tuna still retained their tags after two years at liberty. Differences in shedding rates among skipjack, yellowfin, and bigeye tuna, and differences in shedding rates among taggers were found not to be statistically significant. Tag seeding carried out on board purse seiners by observers resulted in 342 returns of the 532 tags seeded, for a return rate of 64% (60%–68%). The return rate of seeded tags varied significantly by unloading location (most tags were recovered during unloading), but not by species. The highest return rates of seeded tags occurred from American Samoa, Philippines, and Solomon Islands, whereas Korea and Thailand had the lowest return rates. The overall average reporting rate, weighted by the estimated numbers of tags recovered at each location, was 0.59. A bootstrap procedure was used to estimate a 95% confidence interval of 0.49–0.67. These results implied that, of the 146,581 tags released during the large-scale tagging program, 31,166 (27,208–37,264) were recaptured, of which 18,266 were returned to the South Pacific Commission.

Manuscript accepted 17 July 1996.
Fishery Bulletin 95:68–79 (1997).

Tag release-recapture experiments are commonly used to estimate parameters, such as growth, mortality, and population size, of exploited fish stocks (Beverton and Holt, 1957; Seber, 1973). One method used to estimate mortality rates is to fit a tag-attrition model to a time series of tag-return data (Seber, 1973; Kleiber et al., 1987). In its simplest form, the tag attrition model can be expressed as

$$\hat{\phi}_j = (1-\alpha)T \exp\left[-(F+M+\lambda)(j-1)\right]\frac{F}{F+M+\lambda}\left[1-\exp(-F-M-\lambda)\right], \quad (1)$$

where $\hat{\phi}_j$ is the predicted number of tag returns in time period j, α represents all type-1 tag losses, T is the number of tag releases, F is the instantaneous rate of fishing mortality (assumed constant), M is the instantaneous rate of natural mortality (assumed constant), and λ represents all continuous type-2 tag losses. Type-1 tag losses include immediate tag shedding, immediate tagging-induced mortality, and failure to report recovered tags. Type-2 tag losses include continuous tag shedding, continuous mortality directly attributable to the tag, and emigration of tagged fish away from the area of the fishery. For unbiased estimates of F and M to be obtained, it is clear from Equation 1 that these tag losses must be estimated and included in the tag-attrition model.

In general, type-1 and type-2 loss rates cannot be estimated directly from tag-return data, although estimation of type-1 losses may be possible under circumstances where fishing intensity is highly variable (Beverton and Holt, 1957). More commonly, loss rates are estimated from independent experiments carried out in conjunction with a tagging program. Tag-shedding rates may be estimated from double-tagging (two tags per fish) experiments (Wetherall, 1982) or from direct observation of tagged fish held in captivity. Tag-reporting rates may be estimated from tag-seeding experiments (Youngs, 1974; Green et al., 1983; Campbell et al., 1992), from sequential observations of recoveries at different stages of catch handling and processing (Hilborn, 1988), and by comparing tag return rates from the fishery with those from a control group (such as vessels carrying fisheries observers) assumed a priori to report all tag recoveries (Paulik, 1961; Seber, 1973). Type-1 and type-2 tagging mortality rates may, for some species, be estimated from observations of tagged and untagged fish held in captivity.

The South Pacific Commission (SPC) recently conducted a large-

scale tuna tagging program, the Regional Tuna Tagging Project (RTTP), in the western tropical Pacific. From 1989 to 1992, 146,581 tagged skipjack tuna, *Katsuwonus pelamis*, yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *Thunnus obesus*, were released throughout the western tropical Pacific from the Philippines and eastern Indonesia to approximately 170°W. This area is fished by purse-seine, pole-and-line, longline, handline, and troll vessels, which have collectively harvested more than one million metric tons of tuna per year since 1989 (Lawson, 1994). As of 31 May 1995, 18,266 tagged fish had been recaptured and the tags and accompanying recapture information returned to SPC. Tagged tuna were recaptured by all of the fishing methods of the western Pacific fishery. Most tag returns (76%) originated from purse seiners, consistent with the proportion of total catch attributed to that gear (67% for 1990–1993). Few additional tag recoveries are expected.

One of the major objectives of the tagging program was to estimate the rates of fishing-induced and natural mortality by using models similar to Equation 1, so that the impacts of the fishery on the stocks could be assessed. It was therefore necessary to obtain estimates of type-1 and type-2 tag losses. In this paper, I focus on the estimation of tag-shedding rates and tag-reporting rates. Tag-shedding rates were estimated from double-tagging experiments carried out in conjunction with the tag-release program. Differences in shedding rates among species and differences among individual taggers were evaluated. Tag-reporting rates were estimated from tag-seeding experiments in which tuna caught by purse seiners were surreptitiously tagged by fisheries observers prior to the fish being placed in the fish wells. Differences in the rates of reporting seeded tags by species, time, and port of unloading were investigated. An estimate of the overall reporting rate of recovered RTTP tags and its variability, which takes into account the variability in tag reporting among unloading ports, was obtained.

Materials and methods

Double-tagging experiments

Field operations Tagging was carried out on a pole-and-line vessel from which tuna were captured with standard commercial gear. Only uninjured fish that were cleanly hooked in the jaw were selected for tagging. Fish with excessive mouth damage, eye damage, or gill damage were not tagged. Selected fish were placed in a vinyl tagging cradle and their fork lengths measured to the nearest centimeter. For single-tagged fish, a Hallprint™ 13 cm dart tag was inserted by using a sharpened stainless steel applicator, into the musculature at an angle of about 45°, 1–2 cm below the posterior insertion of the second dorsal fin. Smaller (10-cm) tags were used for tuna less than 35 cm FL. Ideally, the tag barb was anchored behind the pterygiophores of the second dorsal fin.

Throughout the three-year tag release program, a small sample (approximately 3%) of the tagged tuna were double tagged. Double tagging occurred on particular days chosen in advance by the cruise leader and on such days, most fish were double tagged. The objectives were for each principle tagger to double tag at least 400 tuna, and for the double-tag releases to be as representative as possible of the species and size composition of the single-tag releases. These objectives were largely accomplished (Fig. 1).

The technique for double tagging was identical to that of single tagging, with the exception that a second tag was inserted on the opposite side of the fish, 1–2 cm anterior to the first tag to avoid damaging it with the applicator. For single and double tagging, fish were generally out of the water for less than ten seconds.

Data analysis Observations of the numbers of tags retained by double-tagged tuna at recapture can be used to estimate tag-shedding rates. I used a simple tag-shedding model (Beverton and Holt, 1957; Hampton and Kirkwood, 1990), which defines the probability, $Q(t)$, of a tag being retained at time t after release as

$$Q(t) = (1-\rho)\exp(-Lt), \tag{2}$$

where ρ is the immediate type-1 shedding rate and L is the continuous type-2 shedding rate. These parameters can be estimated from a double-tagging experiment under the assumption that all tags not immediately shed have identical shedding probabilities that are independent of the status of the companion tag. Given this assumption, the probabilities of two, one, and no tags being retained at time t after release are, respectively,

$$\begin{aligned} P_2(t) &= Q(t)^2, \\ P_1(t) &= 2Q(t)[1-Q(t)] \\ P_0(t) &= [1-Q(t)]^2. \end{aligned} \tag{3}$$

Consider a double-tagging experiment resulting in m recaptures of fish bearing two tags at times t_{2i} (i = 1, ..., m) and in n recaptures bearing one tag at times t_{1j} (j = 1, ..., n). The negative log likelihood of the data ($\mathbf{t}_2$, $\mathbf{t}_1$) given the model parameters ρ and L is

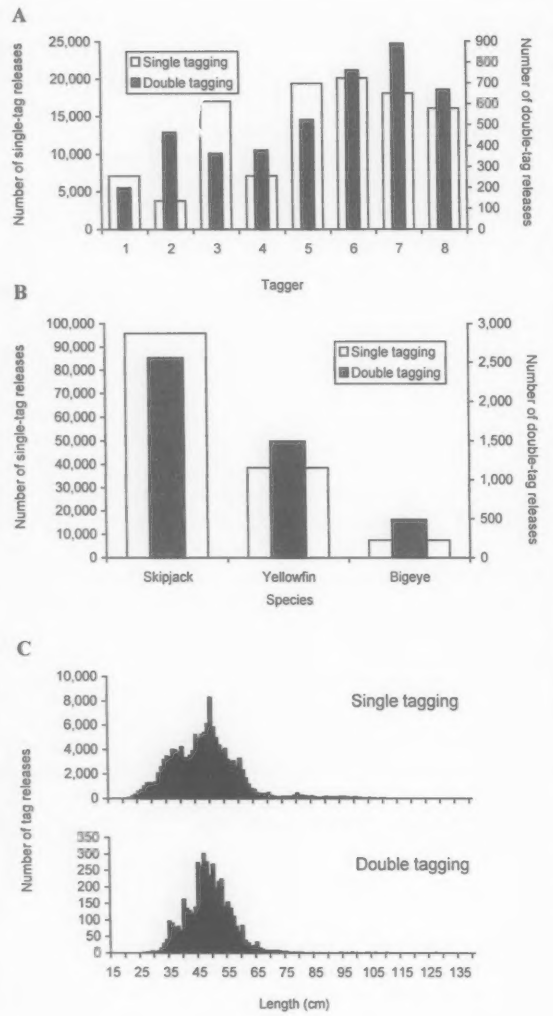


Figure 1

Distributions of single-tag and double-tag releases by (**A**) tagger, (**B**) species and (**C**) size.

$$\Omega(\mathbf{t}_2,\mathbf{t}_1 \mid \rho,L) = -\sum_{i=1}^{m} \ln\left[\frac{P_2(t_{2i})}{1-P_0(t_{2i})}\right] - \sum_{j=1}^{n} \ln\left[\frac{P_1(t_{1j})}{1-P_0(t_{1j})}\right], \quad (4)$$

where the terms in square brackets represent the probabilities of two tags and one tag being observed for each recapture, given that at least one tag is observed. Maximum-likelihood estimates of ρ and L can therefore be obtained by minimizing Ω with respect to the parameters.

The model was fit to pooled recapture data, to data classified by species, and to data classified by tagger. As an approximate indication of the overall losses due to tag shedding for each data set, the proportion of tags retained after two years (99% of RTTP tag returns were recaptured within two years of release), Q_{2yr}, was calculated from Equation 2 by using the estimated parameters. Approximate 95% confidence intervals for Q_{2yr} were obtained by the percentile method (Efron, 1982) applied to distributions of Q_{2yr} generated from 1,000 parametric bootstrap (or Monte Carlo) replicates of each data set. The replicates were constructed by using the observed distributions of times at liberty, and the numbers of tags observed for each pseudo-return were determined randomly with the conditional probabilities of a recaptured tuna bearing two tags or one tag, i.e. $\frac{P_2(t)}{1-P_0(t)}$ and $\frac{P_1(t)}{1-P_0(t)}$, respectively, given the estimated parameters.

The statistical significance of improvements in fit of models that included species-specific and tagger-specific shedding parameters was determined by using likelihood-ratio tests (Kendall and Stuart, 1961).

Tag-seeding experiments

Rationale Tag seeding was carried out by observers placed on board purse-seine vessels as part of regional and national observer programs. The purse-seine fleet was targeted for tag-seeding experiments for several reasons. First, purse seiners account for most of the tuna catch in the western Pacific (and also recovered most tags); the estimation of reporting rates for this gear type in particular was therefore of critical importance. Second, the large, modern purse seiners typical of the western Pacific fleet handle large quantities of tuna very rapidly, with little opportunity for onboard inspection of individual fish for tags. As a result, tagged tuna recaptured by purse seiners were mostly detected during unloading (when individual fish are handled) or during the initial stages of processing in canneries. The efficacy of tag detection during these periods was unknown prior to the commencement of the tagging experiment; it was feared that delayed detection of tags might result in significant losses which, if ignored, would compromise the objectives of the tagging experiment. Third, the very fact that most tagged tuna recaptured by purse seiners

would be detected during or after unloading of the catch in port offered the opportunity for tagged tuna to be planted in the catches before these detection processes began. Furthermore, the layout of purse-seine vessels and the method of onboard handling of the catch facilitated the opportunity for planting tagged tuna surreptitiously, out of sight of the vessel's crew. Such tag-seeding operations would be more difficult on other types of vessels, e.g. pole-and-liners and longliners, operating in the fishery.

Field operations Selected observers on purse seiners were asked to plant up to five tagged tuna in the catch during a voyage. The number of tagged tuna was limited to five so as not to attract undue attention during unloading; it was not unusual during the RTTP for five (and sometimes more) tagged tuna to be recovered from a single unloading. The exact timing of tagging individual fish depended on the circumstances encountered during a cruise, particularly the frequency of successful sets. Therefore, the period over which the five tags were seeded ranged from a few days to several weeks.

Fish were tagged discretely, usually on the well deck (one level below the work deck where the fish are landed), as they passed down the chute just prior to entering the well. The tags and manner of attachment were identical to those used in the tagging program proper. Tag numbers, dates, species, sizes, and well numbers were recorded and the information sent to SPC at the completion of the voyage. Upon recovery, seeded tags were processed in the same fashion as genuine tag recoveries. Tag finders were paid the standard reward for seeded tags and were not informed that the tags were part of a seeding experiment.

Estimation of return rates of seeded tags Return rates of seeded tags were calculated for the overall data set, for the three species (skipjack, yellowfin, and bigeye tuna) and for the seven unloading locations represented in the data (American Samoa, Japan, Korea, Philippines, Puerto Rico, Solomon Islands, and Thailand). For one unloading location (American Samoa), there were sufficient returns to estimate reporting rates by time period (year). Differences in seeded tag-return rates among species, unloading locations, and time periods were assessed by using chi-square tests (Sokal and Rohlf, 1981).

Return rates were estimated by assuming that the number of returns, r, in a given category was a binomial variate. Given the number of tags seeded, N, the estimated return rate is given by $\hat{p} = r/N$. Under these conditions, 95% confidence limits for return rates were also obtained. Lower and upper confidence limits, p_A and p_B, for p were determined by solving the equations

$$\sum_{i=r}^{N} \binom{N}{i} p_A^i (1-p_A)^{N-i} = \alpha \text{ and}$$

$$\sum_{i=0}^{r} \binom{N}{i} p_B^i (1-p_B)^{N-i} = \alpha,$$

where $1-2\alpha$ is the confidence level (0.95 in this instance). Solutions for p_A and p_B can be easily obtained using an optimization program, such as the Microsoft Excel Solver.

Estimation of overall reporting rate for the RTTP An unbiased estimate of the overall return rate of recovered tags (i.e. the total number of tags returned divided by the total number of tags recaptured) is required for the estimation of fishing and natural mortality rates from the RTTP data. The return rates of seeded tags can be considered as sample means of the overall (population) mean reporting rate. It transpired that seeded tag-return rates varied greatly by unloading location, requiring that the data be stratified by unloading location in the estimation procedure. The parametric bootstrap (or Monte Carlo) approach was used to obtain approximate 95% confidence intervals for the overall reporting rate and its components (with the percentile method), taking account of the different probability distributions of reporting rate by unloading location. One thousand simulations (or bootstrap replicates) were run. In each, the weighted average reporting rate across locations is given by

$$p'_{\cdot} = \sum_j R_j \Big/ \sum_j \frac{R_j}{p'_j},$$

where R_j is the number of tags returned from location j and p'_j is the bootstrap (or pseudo) reporting rate for location j.

For each replicate, the p'_j were randomly sampled from probability distributions. For recoveries in locations covered by tag-seeding experiments, beta distributions $B(x_j, y_j, a_j, b)$ were used to represent the probability distributions of the true reporting rates. These continuous distributions are related to the binomial distributions defined by the tag-seeding data by $x_j=r_j$ and $y_j=N_j-r_j+1$ (Mendenhall and Scheaffer, 1973). The limits of the distributions, a and b, would normally be 0 and 1, respectively. In this case, we assumed b=1 and set the lower limit of reporting rate for location j, a_j, to the local tag-return rate (i.e. number of local returns divided by the number of local releases), so as to avoid the possibility of estimated recoveries out-numbering releases for any replicate. For two locations, Solomon Islands and Philippines,

there were local tag releases that resulted in most of the tag returns from those locations. These local tag-return rates (0.126 and 0.223, respectively) were used as the lower bounds for the reporting rate distributions for Solomon Islands and Philippines. For the other locations, it was not possible to identify sets of local releases to calculate local tag-return rates because the release locations of the local returns were widely distributed throughout the tag release area, not just in the vicinity of the unloading ports. In these cases, I made the minimal assumption that the "local" releases comprised all tag releases except those returned from other locations. Thus, the shapes of the reporting-rate probability distributions are determined by the tag-seeding data and by this notional minimum possible return rate. Note that the means and medians of such distributions could be quite different from the tag-seeding sample means $\hat{p}_j$. In general, the differences will be greatest where $\hat{p}_j$ is close to 0 or 1 and n is small.

For returns from locations where no tag-seeding data were available or for tag returns that could not reasonably be pooled with purse-seine returns because the recovery processes were different (14% of all returns), values of p'_j were sampled from uniform distributions $U(0.5,1.0)$. While somewhat arbitrary, this procedure is meant only to reflect some knowledge of the minimum possible reporting rate from these locations. In fact, this assumption probably understates the likelihood of tags being reported; almost all of these tags were recovered in Indonesia and in Pacific Island countries, where widespread publicity and the attractiveness of cash rewards are likely to have resulted in high reporting rates.

Results

Tag shedding

In all, 4,541 tuna (2,557 skipjack, 1,493 yellowfin, and 491 bigeye) were double-tagged during the RTTP. Return rates of double-tagged tuna were comparable to those of single-tagged tuna.

Returns from 525 double-tagged tuna were available for analysis. Fitting the model specified in Equation 2 to the pooled data provided estimates of ρ and L that, according to the model, would result in 89% (95% confidence interval of 82%–94%) of the original tags being retained after two years at large (Table 1). Both $\hat{\rho}$ and $\hat{L}$ were significantly different from zero ($P<0.001$).

Fitting the model to the three species separately, although yielding somewhat different tag-retention rates (Table 1), did not result in an overall statistically significant improvement in fit ($P=0.334$, Table 2). Similarly, there were differences in tag-shedding estimates for the different taggers (Table 1), but over-

Table 1

Double-tagging results (m is the number of returns bearing two tags and n is the number of returns bearing one tag), tag-shedding parameter estimates, the estimated proportion of tags retained after two years at liberty (Q_{2yr}), and likelihood function values (Ω) for fits of the tag-shedding model to the various data sets.

				Tag-shedding parameters				
Data set	$m+n$	m	n	ρ	L (/mo.)	Q_{2yr}	95% confidence interval for Q_{2yr}	Ω
Pooled data	525	457	68	0.05861	0.002312	0.89	0.82–0.94	201.498
Skipjack tuna	241	211	30	0.03485	0.007179	0.81	0.68–0.93	87.637
Yellowfin tuna	204	176	28	0.06574	0.001532	0.90	0.81–0.95	81.434
Bigeye tuna	80	70	10	0.06667	0.000000	0.93	0.74–0.97	30.142
Total	525	457	68					199.213
Tagger 1	42	40	2	0.01111	0.002788	0.92	0.76–1.00	7.909
2	45	36	9	0.07348	0.009636	0.74	0.42–0.93	22.023
3	45	39	6	0.07143	0.003400	0.86	0.76–0.94	17.670
4	53	47	6	0.06000	0.000000	0.94	0.68–0.98	18.718
5	106	94	12	0.03604	0.004257	0.87	0.73–0.96	36.533
6	68	57	11	0.08800	0.000000	0.91	0.70–0.95	30.096
7	81	67	14	0.00000	0.018460	0.64	0.50–0.85	34.184
8	60	53	7	0.03566	0.007403	0.81	0.55–0.97	21.110
Other taggers	25	24	1	0.00000	0.003059	0.93	0.78–1.00	3.600
Total	525	457	68					191.843

all, classification of the model by tagger did not result in a significant improvement in fit (P=0.253, Table 2). It is therefore appropriate to use the parameter estimates for the pooled model in models such as that defined by Equation 1.

Tag reporting

Return rates of seeded tags by species, unloading location, and time period Tag seeding was carried out on 111 observer cruises between May 1990 and September 1994. During these cruises, 532 tuna were tagged and placed in fish wells. Of these, 342 (64%) were later recovered during unloading or processing of catches in canneries. The species breakdown of seeded tag releases and returns is given in Table 3. The numbers of returns by species did not differ significantly from those expected from the return rate pooled across species (P=0.648). On this basis, reporting of tags can be assumed to be independent of species.

Most tag-seeding cruises (77) were undertaken on United States purse seiners because this fleet had the highest observer coverage during the period of the experiment. Tag-seeding cruises were also undertaken on purse seiners from Japan (18), Taiwan (8), Korea (4), Federated States of Micronesia (3), and Solomon Islands (1). It was expected that the tag-reporting rate would vary by fleet, not because of variable cooperation by fishing vessel crews, but because different fleets tend to unload their catches in different ports. As tag detection took place during unloading of catches and at later stages of processing, it was suspected that variation in the effectiveness of tag detection and reporting at unloading ports would result in large differences in tag-reporting rates. The individual tag-seeding cruises were therefore classified by unloading location. In several instances, a vessel's catch was transshipped to two or more ports. In these cases, the seeded tags were classified individually according to the destination of fish in the wells into which the seeded tags had been placed.

The numbers of seeded tag releases and returns, by unloading location, are given in Table 4. The return rates vary considerably among unloading locations; for example, the 95% confidence intervals on the return rates for the two unloading locations with the largest numbers of seeded tags, American Samoa and Thailand, do not overlap and are in fact widely separated. Not surprisingly, the observed numbers of returns by unloading location differed significantly from those expected from the return rate pooled across unloading locations (P<0.001).

For American Samoa, there were sufficient seeded tags to test the hypothesis of constant return rate of seeded tags over time. The return rate was low in 1990 but was consistently high for 1991 through 1994 (Table 5). The differences in return rates among years were statistically significant (P=0.005), but this was due entirely to the lower than expected (on the basis of the return rate pooled across years) number of seeded tags returned in 1990. The differences among years 1991 through 1994 were not statistically significant (P=0.706). Other locations (Japan and Thailand) also had highly variable reporting rates across years, but the numbers of seeded tags for these locations were too few to support a statistical treatment of the data.

Table 2

Statistical tests of the pooled tag-shedding model versus species-specific and tagger-specific tag-shedding models.

Model	No. of parameters	Ω	χ^2	df	P
Pooled	2	201.498			
			4.570	4	0.334
Species-specific	6	199.213			
Pooled	2	201.498			
			19.310	16	0.253
Tagger-specific	18	191.843			

Table 3

Numbers of seeded tag releases and returns, by species. The 95% confidence intervals were calculated assuming a binomial distribution.

Tuna species	Number seeded	Number returned	Return rate	95% confidence interval
Skipjack	333	222	0.667	0.613–0.717
Yellowfin	158	94	0.595	0.514–0.672
Bigeye	35	23	0.657	0.478–0.809
Unknown	6	3	0.500	0.118–0.882
Total	532	342	0.643	0.600–0.684

Table 4

Numbers of seeded-tag releases and returns, by unloading location. The 95% confidence intervals were calculated assuming a binomial distribution.

Unloading location	Number seeded	Number returned	Return rate	95% confidence interval
American Samoa	324	254	0.784	0.735–0.828
Japan	80	39	0.487	0.374–0.602
Korea	16	0	0.000	0.000–0.206
Philippines	5	4	0.800	0.284–0.995
Puerto Rico	16	9	0.562	0.299–0.802
Solomon Islands	5	5	1.000	0.478–1.000
Thailand	86	31	0.360	0.260–0.471
Total	532	342	0.643	0.600–0.684

Table 5

Numbers of seeded tag releases and returns from American Samoa, by year. The 95% confidence intervals were calculated assuming a binomial distribution.

Year	Number seeded	Number returned	Return rate	95% confidence interval
1990	23	3	0.130	0.028–0.336
1991	116	95	0.819	0.737–0.884
1992	50	48	0.960	0.863–0.995
1993	101	83	0.822	0.733–0.891
1994	34	25	0.735	0.556–0.871
Total	324	254	0.784	0.735–0.828

Estimation of overall reporting rate for the RTTP The variation in return rates of seeded tags by unloading location (and possibly over time for some locations) means that the simple, pooled return rate of seeded tags may provide a biased estimate of the overall tag-reporting rate for the RTTP. Therefore, the tag-seeding data were stratified by unloading location, and an overall average reporting rate weighted by the estimated numbers of RTTP tags recovered at those locations was determined. I did not attempt to take into account the possible variation in reporting rates by time because of insufficient information for most locations.

The estimates of the numbers of RTTP tags recovered at various locations and in total are shown in Table 6. Median reporting rates, numbers of tags recovered, and their 95% confidence intervals are based on bootstrap sampling from the reporting-rate probability distributions indicated in Table 6. The relationships between the bootstrap distributions and the sample means $\hat{p}_j$ from tag seeding are shown in Figure 2. For some locations, notably Philippines and Solomon Islands, $\hat{p}_j$ overestimates the median of the probability distribution of p_j. This is due to the small numbers of seeded tags in these locations and the resulting effect on the shape of the assumed underlying probability distributions.

The estimation of tag recoveries and reporting rates for Korea and Taiwan had to be treated differently because no RTTP tags were returned from Taiwan and only four tags were returned from Korea (which were given to a SPC staff member during a brief visit). Additionally, it was not possible to seed tagged fish into shipments bound for Taiwan. Therefore, there was no basis for estimating tag recoveries and reporting rates in Korea and Taiwan directly from tag-seeding and RTTP tag-return data.

However, other information was available to derive estimates for these locations. During the period of the RTTP, approximately 100,000 t of tuna was processed annually by canneries in Korea, all of which was supplied by Korean purse seiners (Lewis[1]).

[1] Lewis, A.D. 1993. Product flows of tuna in the western Pacific, 1991 with likely trends during 1992. Sixth standing committee on tuna and billfish; 16–18 June 1993, Pohnpei, Federated States of Micronesia, South Pacific Commission, Noumea, New Caledonia. Information paper 2, 7 p.

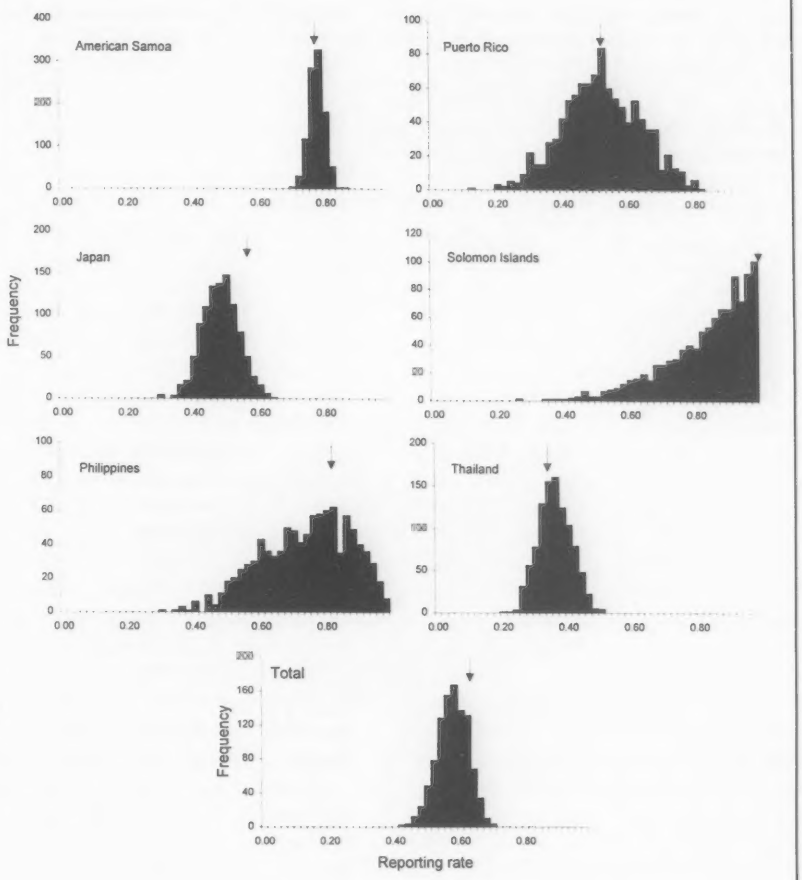


Figure 2

Frequency distributions of reporting rates p'_j sampled from the probability distributions specified in Table 6. The arrows indicate values of the sample mean reporting rates $\hat{p}_j$ obtained from tag-seeding data. The number of observations in each distribution is 1,000.

A similar quantity of the Korean purse-seine catch in the western Pacific was delivered to canneries in Thailand. Assuming a similar occurrence of tagged tuna in these components of the Korean catch, the number of tagged tuna in catches delivered to Korea can be approximated by the tag returns from Korean purse seiners unloading in Thailand (658) divided by the estimated reporting rate for Thailand (0.355). On this basis, 1,798 (95% confidence interval of 1,412–2,386) tagged tuna are estimated to have been landed in Korea, of which only four were returned to SPC under the special circumstances described above. Similarly, the disposition of the Taiwanese purse-seine catch (approximately 20,000 t to Taiwan and 155,000 t to Thailand annually) and tag returns from Taiwanese purse seiners unloading in Thailand (928) implies that 327 (257–434) tagged tuna were present in catches delivered to Taiwan.

Summing across locations, it is estimated that 31,166 (27,208–37,264) RTTP tags were recovered from all fisheries in the western Pacific, resulting in an overall reporting rate of 0.586 (0.490–0.671).

Discussion

The objective of this study was to quantify two sources of tag loss, tag shedding and failure to re-

Table 6

Numbers of tags returned and estimates of numbers of tags recovered from various unloading locations. Median reporting rates, median numbers of tags recovered, and their respective 95% confidence intervals, were determined from 1,000 bootstrap replications based on random sampling from the specified beta (B) or uniform (U) distributions. Parameters for the beta distributions $B(x,y,a,b)$ are $x=r$, $y=N-r+1$, where N is the number of tags seeded, r is the number of seeded tags returned, a is the minimum possible reporting rate (based on the local tag-return rate), and b is the maximum possible reporting rate (1). The estimations for Korea and Taiwan could not be carried out in the usual way because of zero or very small numbers of seeded or RTTP (or both) tag returns. Estimations for these locations are described fully in the text.

		Reporting rate			Number of tags recovered	
Unloading location	Number of tags returned	Probability distribution	Median	95% confidence interval	Median	95% confidence interval
American Samoa	2,070	$B(254,71,0.016,1)$	0.784	0.739–0.826	2,639	2,505–2,802
Japan	1,969	$B(39,42,0.015,1)$	0.492	0.386–0.595	4,000	3,307–5,104
Korea	4		0.002	0.002–0.003	1,798	1,412–2,386
Philippines	6,671	$B(4,2,0.223,1)$	0.764	0.476–0.961	8,727	6,940–14,003
Puerto Rico	297	$B(9,8,0.002,1)$	0.525	0.301–0.753	565	395–988
Solomon Islands	2,226	$B(5,1,0.126,1)$	0.877	0.526–0.994	2,540	2,239–4,232
Taiwan	0		0.000	0.000–0.000	327	257–434
Thailand	2,218	$B(31,56,0.017,1)$	0.366	0.276–0.466	6,061	4,761–8,043
Tagging vessel	243		1.000	1.000–1.000	243	243–243
Other	2,568	$U(0.5,1.0)$	0.746	0.518–0.987	3,442	2,601–4,956
Total recoveries	18,266		0.586	0.490–0.671	31,166	27,208–37,264

port tags, in a large-scale tuna tagging experiment in the western tropical Pacific Ocean.

Tag-shedding rates were estimated by fitting a tag-shedding model to double-tagging data. The application of a double-tagging experiment to the estimation of the rate at which tags are shed from single-tagged fish requires several assumptions that are discussed in detail by Beverton and Holt (1957). In this study, there are four assumptions that warrant discussion. First, it must be assumed that the shedding rates of tags applied in the double-tagging experiment are the same as those for single-tagged fish. This assumption might fail if, for example, less care was taken with double tagging than with single tagging because of the need to return fish to the water within certain time limits. In the RTTP tagging experiment, taggers were instructed to take as much care in implanting each tag in double-tagged tuna as they would for single-tagged tuna. Although it is not possible to test this assumption with the limited amount of double-tagging data, the similarity in return rates of double- and single-tagged tuna (South Pacific Commission[2]) suggests that there had not been a gross violation. If the assumption did fail, as described above, the shedding rates as applied to single-tagged tuna would be overestimated.

Second, it is necessary to assume for double-tagged fish that the events potentially resulting in shedding of tags are random and independent with respect to the two tags. If this assumption fails, there will be fewer observations of fish retaining one tag, and consequently shedding rates will be underestimated. This assumption is difficult to test unless it is possible to identify fish that have shed both tags, which of course will not normally be the case under field conditions. The techniques adopted in this experiment (individual tag placement on opposite sides of the fish) were designed to facilitate compliance with this assumption, but the actual extent of compliance remains unknown.

Third, it must be assumed that the first (primary) and second (companion) tags applied to fish in a double-tagging experiment have the same probabilities of shedding. This assumption might fail if, for example, the companion tag is less securely implanted because tagging on the opposite side of the fish is an unfamiliar task. This assumption can be tested by using the frequencies of primary and companion tag retention in fish that were recaptured bearing one tag. In this double-tagging experiment, there were 68 returns that consisted of one tag. Of

[2] South Pacific Commission. 1994. Oceanic Fisheries Programme work programme review 1993–94 and work plan 1994–95. Seventh standing committee on tuna and billfish; 5–8 August 1994, Koror, Palau, South Pacific Commission, Noumea, New Caledonia. Working paper 5, 66 p.

these, 29 returns were of the primary tag and 39 were of the companion tag. The cumulative binomial probability of 29 or less of either the primary or companion tag being found in a sample size of 68 is 0.275, indicating that there is a reasonable chance of the assumption being satisfied.

Fourth, in the analysis carried out here, it was assumed that tag pairs (from fish recovered with two tags) are reported (or not) as a pair—i.e. either both, or none are reported. Furthermore, it was assumed that the probability of reporting a tag pair was the same as that of reporting a single tag. I will refer to this as the dependent hypothesis. An alternative hypothesis is that the reporting of individual tags forming a pair is completely independent; whether or not one tag of a pair is reported has no effect on the probability that the other will be reported. I will refer to this as the independent hypothesis. Under either hypothesis, we can define the probability, $U(t)$, that a tag is retained at recapture time t and is reported as

$$U(t) = pQ(t \mid \rho, L) = p(1-\rho)\exp(-Lt). \qquad (2a)$$

However, the probabilities of two, one, and no tags being retained at recapture time t, and, in the case of at least one tag being retained, also reported, are different under the two hypotheses, as follows:

$$\begin{aligned} P_{d2}(t \mid \rho_d, L_d) &= pQ(t \mid \rho_d, L_d)^2 \\ P_{d1}(t \mid \rho_d, L_d) &= 2pQ(t \mid \rho_d, L_d)\left[1 - Q(t \mid \rho_d, L_d)\right] \\ P_{d0}(t \mid \rho_d, L_d) &= pQ(t \mid \rho_d, L_d)^2 - 2pQ(t \mid \rho_d, L_d) + 1 \end{aligned} \qquad (3a)$$

and

$$\begin{aligned} P_{i2}(t \mid \rho_i, L_i) &= p^2 Q(t \mid \rho_i, L_i)^2 \\ P_{i1}(t \mid \rho_i, L_i) &= 2pQ(t \mid \rho_i, L_i)\left[1 - pQ(t \mid \rho_i, L_i)\right] \\ P_{i0}(t \mid \rho_i, L_i) &= \left[1 - pQ(t \mid \rho_i, L_i)\right]^2, \end{aligned} \qquad (3b)$$

where the d and i subscripts indicate the dependent and independent hypotheses, respectively.

It can be shown that substitution of the right-hand sides of Equations 3a into the log-likelihood Equation 4 produces an identical result to substitution of Equation 3; the p's cancel out and reporting rate has no influence on the estimates $\hat{\rho}_d$ and $\hat{L}_d$ when the dependent hypothesis is true. This is therefore equivalent to using Equation 2 as the tag-shedding and reporting model, as I have done in this study.

Under the independent hypothesis, substitution of the right-hand sides of Equations 3b into the log-likelihood Equation 4 does not result in a canceling out of p terms, and therefore p must be included in the tag-shedding and reporting model as shown in Equation 2a. However, p is totally confounded with $1-\rho_i$, and cannot be estimated from the double-tagging data. If an independent estimate of p is available (for example, from a tag-seeding experiment), Equation 2a can be applied and ρ_i estimated free of the effects of p.

For most double-tagging experiments, it will not be known with any certainty whether the dependent or independent hypothesis is more appropriate. The following procedure may provide some insight in this regard:

1 Obtain tag-shedding parameter estimates $\hat{\rho}_d$ and $\hat{L}_d$, assuming that the dependent hypothesis is true (using Equations 2 and 3).
2 If an independent estimate of the reporting rate, $\hat{p}$, is available, obtain tag-shedding parameter estimates $\hat{\rho}_i$ and $\hat{L}_i$, assuming that the independent hypothesis is true (using Equations 2a and 3b). Small values of $\hat{p}$ (less than $1-\hat{\rho}_d$) will usually result in $\hat{\rho}_i$ entering an unreasonable (negative) domain. Alternatively, if $\hat{\rho}_i$ is constrained to be nonnegative, $\hat{L}_i$ will differ from $\hat{L}_d$ and the fit to the data will degrade (i.e. $\Omega_i > \Omega_d$). In either case, this indicates inconsistency between the reporting rate estimate $\hat{p}$ and the independent hypothesis. In the present study, the estimated reporting rate (0.586) was much smaller than $1-\hat{\rho}_d$ (0.941, see Table 1). If $\hat{p}$ is applicable to the double-tagged tuna, this implies that the independent hypothesis is inappropriate for these data.

In reality, it is likely that the actual situation with respect to the reporting of tag pairs will lie somewhere between completely dependent and completely independent reporting. It is possible to generalize the tag-shedding model with respect to these hypotheses by defining a coefficient of independence, c, such that

$$U(t) = \frac{p(1-\rho)\exp(-Lt)}{c(1-p)+p}.$$

Setting c=0 is equivalent to the dependent hypothesis, c=1 is equivalent to the independent hypothesis, while $0<c<1$ implies partial independence. For the RTTP double-tagging data and $\hat{p} = 0.586$, $c<0.088$ allows an unconstrained $\hat{\rho}$ to remain nonnegative. This range of possible values of c implies that the dependent hypothesis is likely to be appropriate for these data.

The tag-shedding model fitted to the double-tagging data assumes that the rate of tag shedding is constant over time. Kirkwood (1981) and Hampton and Kirkwood (1990) found that, in some cases, a model that allowed the probability of shedding to

decrease over time provided a better fit to double-tagging data for southern bluefin tuna, *Thunnus maccoyii*, than the model used in this study. They reasoned that tags might become more securely fixed over time, and thus less likely to be shed, as the fish grows and tissue is built up around the tag shaft. I fitted the three-parameter variable-rate shedding model (model 4 in Hampton and Kirkwood [1990]) to the pooled data set and to the three species-specific data sets and found that the improvement in fit over the constant shedding-rate model was negligible in each case and did not warrant the addition of the extra parameter. There is thus little evidence of a decline in shedding rates over time in these data. This may in part be due to the relatively short periods at liberty (maximum of 2 years) of the double-tagged tuna in this study compared with those for the southern bluefin tuna (up to 18 yr) analyzed by Hampton and Kirkwood (1990).

Given compliance with the assumptions of the experiment and the appropriateness of the model, it can be concluded that losses of tags through shedding are relatively modest (about 11% after two years) for the RTTP. This shedding rate is comparable to those reported by Hampton and Kirkwood (1990) for the more recent southern bluefin tuna double-tagging experiments (16% and 12% after two years for experiments 7 and 8, respectively), where comparable tags and techniques to those used in this experiment were used. Other tuna tagging experiments have reported substantially higher tag losses after two years, e.g. 30%–50% for the early southern bluefin tuna experiments (Hampton and Kirkwood, 1990), 43% for eastern Pacific yellowfin tuna (Bayliff and Mobrand, 1972), and 35% for Atlantic bluefin tuna (Lenarz et al., 1973; Baglin et al., 1980). It is possible that the higher shedding rates observed in some of these experiments were due to inferior tags, in which the streamers were prone to detach from the tag head. The streamers of tags used in this experiment and the recent southern bluefin tuna experiments were heat fused to the tag heads, making detachment impossible under normal conditions.

The analysis of tag-seeding and associated data indicated that, despite extensive publicity and attractive rewards for tag finders, failure to report tags was a significant source of tag loss in the RTTP. Given the diverse nature of the fishery, its spatial extent, and the methods of processing large quantities of fish caught by purse seiners in particular, this is hardly surprising. The estimated overall reporting rate in fact compares more than favorably with those for some tagging experiments carried out on more local scales (e.g. Campbell et al., 1992 for coastal shrimp in the Gulf of Mexico). My estimates of reporting rates based on tag-seeding data may, if anything, err on the pessimistic side. It is suspected that one cause of failure to report purse-seine–caught tagged tuna may be the detachment of tags (through abrasion) from fish while they are held in the vessels' wells. If this occurs, detached tags would likely be flushed out of the wells into the sea, after which detection would be highly improbable. It is possible that tags placed in dead tuna by observers were more prone to detachment in the well than tags placed in live tuna that had been at liberty for some time. The tag head and the portion of the tag shaft imbedded in the musculature of live tuna were frequently observed to be encased in a fibrous capsule, which would tend to fix the tags more securely than tags placed in dead tuna. "Shedding" of seeded tags could conceivably result in losses of seeded tags of the same order as, or greater than, the immediate tag-shedding rates estimated from the double-tagging experiment on live tuna (about 6%). It may be possible to estimate the extent of this problem by conducting a double-tagging experiment for seeded tags.

The main purpose of estimating tag-shedding and reporting rates is to allow these processes to be incorporated into analyses of the tagging data for the purpose of estimating mortality rates. Typically, this would involve substitution of the point estimates of the parameters into equations such as Equation 1; mortality rates that are free of the effects of these tag losses could then be estimated from the tagging data (e.g. Kleiber et al., 1987). However, where the ultimate objective of the analysis (mortality rate estimation) is stock assessment related, it is important to have not only estimates of the mean rates but also estimates of their precision that are unconditional on estimates of nuisance parameters such as tag-shedding and reporting rates.

In this study, estimates of precision (expressed as 95% confidence intervals) of tag-shedding and reporting rates were obtained by using the percentile method applied to the bootstrap distributions of the parameter estimates. For the tag-shedding analysis, I confined this to estimates of precision of Q_{2yr}, although confidence intervals for the model parameters could be similarly derived. The advantage of the bootstrap approach as applied to the analysis of tag reporting is that it allowed the precision of the overall reporting rate to be easily determined given some knowledge, or reasonable assumptions, regarding the reporting-rate probability distributions for differing components (in this case, based on unloading location) of the data set. The approach also provided a convenient means of integrating uncertainties in tag-shedding and reporting rates (via the individual bootstrap values) into a similarly structured bootstrap

procedure for the estimation of mortality rates from the overall RTTP tagging data. The precision of the mortality rates estimated with such a procedure will then incorporate uncertainties in the estimates of tag-shedding and reporting rates and not be conditional on point estimates of these parameters.

Acknowledgments

The RTTP and associated experiments were supported by a grant from the Commission of the European Communities Sixth European Development Fund. Special thanks are due to Gordon Yamasaki and Craig Heberer, who coordinated the placement of observers, distributed tag-seeding equipment, and briefed observers on the requirements of the experiment. The manuscript was improved considerably by the comments of three anonymous reviewers.

Literature cited

Baglin, R. E., Jr., M. I. Farber, W. H. Lenarz, and J. M. Mason Jr.
1980. Shedding rates of plastic and metal dart tags from Atlantic bluefin tuna, *Thunnus thynnus*. Fish. Bull. 78:179–185.

Bayliff, W. H., and L. M. Mobrand.
1972. Estimates of rates of shedding of dart tags from yellowfin tuna. Inter-Am. Trop. Tuna Comm. Bull. 15:465–503.

Beverton, R. H. J., and S. J. Holt.
1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II, Mar. Fish. G.B. Minist. Agric. Fish. Food 19, 533 p.

Campbell, R. P., T. J. Cody, C. E. Bryan, G. C. Matlock, M. F. Osborn, and A. W. Green.
1992. An estimate of the tag-reporting rate of commercial shrimpers in two Texas bays. Fish. Bull. 90:621–624.

Efron, B.
1982. The Jackknife, the bootstrap and other resampling schemes. Society for Industrial and Applied Mathematics, Philadelphia, 92 p.

Green, A. W., G. C. Matlock, and J. E. Weaver.
1983. A method for directly estimating the tag-reporting rate of anglers. Trans. Am. Fish. Soc. 112:412–415.

Hampton, J., and G. P. Kirkwood.
1990. Tag shedding by southern bluefin tuna *Thunnus maccoyii*. Fish. Bull. 88:313–321.

Hilborn, R.
1988. Determination of tag return from recaptured fish by sequential examination for tags. Trans. Am. Fish. Soc. 117:510–514.

Kendall, M. G., and A. Stuart.
1961. The advanced theory of statistics. Vol. 2: Inference and relationship. Charles Griffin, London, 676 p.

Kirkwood, G. P.
1981. Generalized models for the estimation of rates of tag-shedding by southern bluefin tuna (*Thunnus maccoyii*). J. Cons. Int. Explor. Mer 39:256–260.

Kleiber, P., A. W. Argue, and R. E. Kearney.
1987. Assessment of Pacific skipjack tuna (*Katsuwonus pelamis*) resources by estimating standing stock and components of population turnover from tagging data. Can. J. Fish. Aquat. Sci. 44:1122–1134.

Lawson, T. (Ed.)
1994. Tuna fishery yearbook 1993. South Pacific Commission, Noumea, New Caledonia, 81 p.

Lenarz, W. H., F. J. Mather III, J. S. Beckett, A. C. Jones, and J. M. Mason Jr.
1973. Estimation of rates of tag shedding by northwest Atlantic bluefin tuna. Fish. Bull. 71:1103–1105.

Mendenhall, W., and R. L. Scheaffer.
1973. Mathematical statistics with applications. Duxbury Press, North Scituate, MA, 561+88 p.

Paulik, G. J.
1961. Detection of incomplete reporting of tags. J. Fish. Res. Board Can. 18:817–832.

Seber, G. A. F.
1973. The estimation of animal abundance and related parameters. Charles Griffin, London, 654 p.

Sokal, R. R., and F. J. Rohlf.
1981. Biometry. W. H. Freeman, San Francisco, CA, 859 p.

Wetherall, J. A.
1982. Analysis of double-tagging experiments. Fish. Bull. 80:687–701.

Youngs, W. D.
1974. Estimation of the fraction of anglers returning tags. Trans. Am. Fish. Soc. 103:616–618.

Use of gonad indices to estimate the status of reproductive activity of female swordfish, *Xiphias gladius*: a validated classification method

Michael G. Hinton

Inter-American Tropical Tuna Commission
8604 La Jolla Shores Drive, La Jolla, California 92037-1508

Ronald G. Taylor

Michael D. Murphy

Florida Marine Research Institute, Florida Department of Environmental Protection
100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095

Abstract.—Gonad weights and results of histological analyses from 85 swordfish, *Xiphias gladius*, were used to develop a validated method for classification of the reproductive activity of female swordfish based on gonad indices (GI's). The validated method provides a significant improvement over previously published (unvalidated) methods. The method was shown to be independent of the length of individual fish, important when length is used as a criterion for selection of individuals from which summary statistics based on GI are being developed. Female swordfish were found to be in a reproductively active condition when GI = ln(gonad weight in gm)/ln(eye-fork-length in cm) ≥ 1.375. Classification methods for species with comparable reproductive habits and characteristics may be alike, and it is speculated that results for other billfishes would be similar to those described for swordfish.

Manuscript accepted 12 August 1996.
Fishery Bulletin 95:80–84(1997).

We describe a validated classification method that uses gonad indices (GI's) to determine accurately the reproductive condition of female swordfish, *Xiphias gladius*. This study uses previously unpublished data as well as histological analyses detailed in Taylor and Murphy's (1992) study of the reproductive biology of swordfish captured in the Straits of Florida. It is standard practice to use GI's to identify regions and times of active spawning in studies of the distribution and structure of stocks of many species of fish, including swordfish (e.g. Kume and Joseph, 1969; Shingu et al., 1974; Miyabe and Bayliff, 1987; Sosa-Nishizaki, 1990; Nakano and Bayliff, 1992; Arocha and Lee, 1993; Arocha et al., 1994; Gouveia and Mejuto, 1994; Arocha and Lee, 1995; Hinton and Deriso, in press). Data on the reproductive activity of swordfish are costly and difficult to obtain but essential to studies such as those noted; full use should be made of all available information. Our classification method overcomes problems of published methods (e.g. Miyabe and Bayliff, 1987), which have the potential to reduce the information database of the researcher by over 50%. To our knowledge, it is the first method applicable to female swordfish to have been validated with data obtained from histological analyses, which provide a verifiable measure of the reproductive status of individual swordfish.

The standard practice (Gouveia and Mejuto, 1994) in studies using values of GI for female swordfish has been to estimate $GI = 10^4 \times GW/EFL^3$, where GW = gonad weight in grams, and EFL = length from the posterior edge of the orbit to the fork of the tail in centimeters (we note that without loss of generality, other length measurements, such as lower-jaw fork length (LJFL), have been used) (Kume and Joseph, 1969). The latter assumed that "[females] with gonad indices equal to or greater than 3 are about to spawn." Miyabe and Bayliff (1987) modified their method by assuming that "only females with gonad indices of 7.0 or greater were [about to spawn]." Arocha and Lee (1995) modified the method of Kume and Joseph (1969) when they noted that females with GI's greater than 4.0 were in prespawning condition. In certain applications of these methods, e.g. comparison of average GI's for different regions or time periods,

it is necessary to ensure that the averages being compared are for individuals with comparable reproductive potential or maturity. Thus, it is standard practice to use a minimum length (e.g. Miyabe and Bayliff, 1987; Sosa-Nishizaki, 1990; Nakano and Bayliff, 1992, Arocha et al., 1994; Arocha and Lee, 1995) to decide which data to include in estimates of average values of GI, making it important to document that minimum-length criteria have no impact on methods used to estimate reproductive status (Cayré and Laloë, 1986).

Data and methods

Details on data collection and histological analyses, other than estimation of the values of individual gonad indices, may be found in Taylor and Murphy (1992). Female swordfish were assigned to eight developmental classes (Murphy and Taylor, 1990) based on the appearance of histological features (Wallace and Selman, 1981). These classes and mean observed oocyte diameters were 1) immature, < 20 μmm; 2) developing, 71 μmm; 3) maturing, 160 μmm; 4) mature, 434 μmm, 5) gravid, 723 μmm; 6) spawning or partially spent, 823 μmm; and 7) spent, 181 μmm. Individuals in class 8 (recovering) were observed but not described in Taylor and Murphy (1992). Gonads of swordfish in class 8 exhibited signs of having spawned in the previous season and were undergoing maturational, prespawning development for subsequent reproductive efforts.

The preferred formulation for GI may be determined by examining the relation of gonad weight to measures of body size (de Vlaming et al., 1982). The formulation chosen should meet the underlying assumptions (de Vlaming et al., 1982) for use of GI as an index of reproductive status. In addition to examining the previously described "standard" expression of GI (hereafter referred to as GI(1)), we examined $GI = \ln(GW)/\ln(EFL)$, hereafter referred to as GI(2), and $GI = GW/EFL$. Stepwise analysis of covariance (ANCOVA) was used to examine how well these formulations for GI met the underlying assumptions (de Vlaming et al., 1982) for use of GI as an index of the reproductive status of female swordfish. Values of GI were determined for the fish for which histological data had been obtained. For those individuals for which measurements of EFL were not obtained, measurements of LJFL were used to estimate EFL as follows: $EFL = -8.259 + 0.930 \times LJFL$ [n=316, r^2=0.996, P<0.001] (Taylor and Murphy, 1992). Of the over 400 fish examined by Taylor and Murphy (1992), there were 85 individuals (Table 1) with measurements (40) or estimates (45) of EFL ranging from 73 to 253 cm, for which there were GW's and data from

Table 1

The status of reproductive activity (R) of swordfish determined by histological analyses [Taylor and Murphy, 1992]), EFL = eye fork length (cm), and GW = gonad weight (gm).

R	GW	EFL	R	GW	EFL	R	GW	EFL	R	GW	EFL
2	3	77	2	100	113	3	752	169	6	8,740	221
2	13	86	2	110	147	4	530	161	6	8,840	208
2	14	88	2	135	115	4	780	182	6	9,920	206
2	15	94	2	140	118	4	800	187	6	10,180	188
2	30	96	2	140	128	4	1,320	186	6	10,430	227
2	30	95	2	150	121	4	2,140	219	6	11,340	223
2	30	92	2	220	93	4	2,888	201	6	15,140	253
2	35	97	2	225	73	5	2,690	169	8	446	167
2	35	99	2	255	148	5	3,950	184	8	540	172
2	35	106	3	100	121	6	1,240	181	8	600	166
2	35	106	3	105	130	6	1,540	202	8	640	164
2	37	101	3	110	123	6	1,760	174	8	730	183
2	45	114	3	200	137	6	2,270	182	8	800	190
2	50	99	3	240	139	6	3,650	181	8	980	179
2	50	96	3	300	168	6	3,780	171	8	995	197
2	55	104	3	353	166	6	3,850	208	8	1,325	200
2	70	103	3	437	120	6	3,900	155	8	1,340	222
2	70	105	3	470	184	6	4,000	180	8	1,360	249
2	80	104	3	500	181	6	4,700	191	8	1,500	211
2	80	112	3	620	185	6	4,720	197	8	1,790	191
2	90	113	3	680	186	6	6,034	154			
2	100	128	3	680	174						

histological analyses. According to the results of the histological analyses, swordfish were considered to be in spawning condition, i.e. spawning was in progress or imminent in the region in which the fish was captured, if they were either "gravid" or "spawning or partially spent" (classes 5 and 6 of Taylor and Murphy [1992]). Individuals in these conditions were classified as in an active (A) reproductive status. All others were classified as quiescent (Q).

In our study the results of histological analyses represent the known reproductive status of individual swordfish, and the H(i) are various hypothesized classification methods (Table 2) for placing swordfish into categories A or Q. In some cases, these H(i) indicate minimum-length criteria used to determine which data from individual swordfish should be included in estimates of average values of GI. To facilitate the examination of impacts of minimum-length criteria on classification methods, these criteria were treated as a component of the H(i) in our analyses. We do not attempt to define minimum-length criteria for size at maturity in this study (cf. Taylor and Murphy [1992]); our concern was to determine if classification methods based on GI were independent of such criteria. The hypotheses identified in Table 2 as "Present study" are representative of a multitude of hypotheses we examined.

The optimum value (OV) and confidence intervals for the value of GI to be used as criteria, GI*, to estimate the reproductive condition of individual female swordfish were determined by using maximum-likelihood estimation procedures and the following model:

Let $R = 1$ if a swordfish is reproductively active (classes 5 and 6 of Taylor and Murphy [1992]), otherwise $R = 0$. Then for individual fish, i, selected at random,

P (a swordfish is reproductively given its gonad index) $= \pi(GI)^R \times (1 - \pi(GI))^{(1-R)}$.

Maximum-likelihood estimates of $\pi(GI)$ are given by the number of successes in the series of trials determined by the value of GI^* in the data, divided by the number of trials. Thus, for our data set: $[GI_1, ..., GI_k^*, ..., GI_n]$ and $[R_1, ..., R_k, ..., R_n]$ = [the observed values of GI] and [the respective measure of reproductive status determined by histological analyses] for individual fish, these estimates are given by

$$\pi(GI) = \begin{cases} \dfrac{\text{(number of individuals with } R = 1 \text{ and } GI < GI_k^*)}{k-1} & \text{for individuals with } GI < GI_k^* \\ \dfrac{\text{(number of individuals with } R = 1 \text{ and } GI \geq \mathrm{GI}_k^*)}{n-k+1} & \text{for all others} \end{cases}$$

It follows that the optimum value, GI^*, is that which maximizes the following log-likelihood function ($LKLHD$):

$$LKLHD = \sum \left[R \times \ln(\pi(GI)) + (1-R) \times \ln(1-\pi(GI)) \right]$$

Results and discussion

Results of classifying individuals as either A or Q based on the results of the histological analyses and from application of the various H(i) (treated in each test as the null hypothesis) are given in Table 3. It is clear that H(2) and H(3) fail to classify individuals correctly according to reproductive status as determined by histological analyses. Under H(2) and H(3), individuals below the minimum-length criteria are not classified. About 75% of the individuals whose lengths were above the size restrictions stated in these hypotheses were classified correctly, but only 48% of the individuals in this group that were reproductively active were correctly classified which represents a significant type-1 error that may be extremely costly in terms of loss of information on the distributions of reproductively active swordfish. However, this is a result of the value of GI included in the hypotheses and not a result of restrictions placed on lengths of individuals included in the analyses, as is evidenced by the results for the other H(i). We also note that length was not found to be a signifi-

Table 2

Levels of gonad indices (GI) used to classify the reproductive activity of female swordfish and minimum eye fork length (EFL) criteria used to standardize statistics for comparison among areas and times, as employed by various researchers. Formulations for GI(1) and GI(2) are given in the text.

H(i)	Classification method	Author
1	GI(1) ≥ 3.0	Kume and Joseph
2	GI(1) ≥ 7.0 and EFL > 150 cm	Miyabe and Bayliff
3	GI(1) ≥ 7.0 and EFL > 160 cm	Sosa-Nishizaki
4	GI(1) ≥ 4.0 and EFL > 131 cm[1]	Arocha and Lee
5	GI(1) ≥ 6.0	Present study
6	GI(2) ≥ 1.37	Present study

[1] Authors used lower-jaw fork length >150 cm.

Table 3

Comparison between the correct (from histological analyses [HA] of the ovaries) and estimated (from GI's) classification of reproductive status of female swordfish. Individuals were classified as reproductively active (A) or quiescent (Q). Asterisks designate incorrect classifications based on GI's, IC is the percentage of all individuals [*n* determined by H(i)] classified correctly, and AC is the percentage of reproductively active individuals, within the *n* individuals, that were classified correctly.

H(i)	*n*	HA	GI A	GI Q	IC	AC
1	85	A	19	2*	95.3	90.5
		Q	2*	62		
2	48	A	10	11*	77.1	47.6
		Q	0*	27		
3	46	A	10	11*	76.1	47.6
		Q	0*	25		
4	52	A	17	4*	92.3	81.0
		Q	0*	31		
5	85	A	15	6*	92.9	71.4
		Q	0*	64		
6	85	A	21	0*	95.3	100.0
		Q	4*	60		

cant term in logistic regressions that included EFL as a classification variable.

Under H(1) and H(6), 95% of the 85 individuals were classified correctly (Table 3); further, under H(6) all individuals that were reproductively active were correctly classified, which was significantly (see following discussion) more than the 91% of the reproductively-active individuals correctly classified under H(1) and the 71% to 81% correctly classified under H(5) and H(4), respectively. Hypothesis H(6) placed about 4.7% of the individuals that were quiescent in the active category, and H(1), about 2.5%, both of which represent relatively low rates of type-2 error.

Although length-cubed is often the choice to standardize GW, as in the "standard" expression for GI, length is also frequently used. Further, GW may be exponentially related to body size (de Vlaming et al., 1982), in which case log transformation as in GI(2) is indicated. We examined these hypotheses in formulations of GI for female swordfish. The results of ANCOVA revealed significant ($P<0.01$) heterogeneity among slopes and intercepts of the regressions of GW on EFL and on EFL^3 for reproductive classes (2, 3, 4, [5, 6] and 8) of Taylor and Murphy (1992). At the same time, ANCOVA on the log-transformed data yielded only one significant ($P<0.01$) coefficient, that for the intercept of class (5, 6); however this coefficient was only about 28% of the estimated intercept of the overall regression. Thus, the formulation of the gonad index that best conformed to the underlying assumptions (de Vlaming et al., 1982) was GI(2). In addition, the maximum-likelihood test based on the values of LKLHD for the difference between methods showed that model GI(2) provided a significant ($\chi^2(1)$, $P=0.033$) improvement over model GI(1). The estimate of OV obtained from maximum-likelihood analyses for *GI*(2) was ($1.366 < OV < 1.375$). Note that although GI(2) has a continuous distribution, the interval estimate of OV is a function of the distribution of values of GI(2) in the sample data, and thus any hypothesized value in this range would yield LKLHD and tabled results identical to those shown for H(6). Further, because the solution for the function LKLHD is so knife-edged, the estimate of OV includes the 90% confidence interval, and the 95% confidence interval for the estimate of OV, ($1.357 < OV < 1.375$), differs only in the lower bound.

Two points should now be clear. First, the classification methods that are based on GI(1) that have been used and published in studies requiring estimates of the reproductive status of female swordfish do not meet the underlying assumptions (de Vlaming et al., 1982) for use as an indicator of reproductive status, and they may also be viewed in some instances as overly restrictive, in that they may have excluded significant amounts of usable data from analyses that were already hampered by limited information. This resulted, at least in part, from using values of GI that corresponded to a fully ripe and running condition of the gonad. Second, the classification methods, both previously published and described herein, were not impacted by minimum-length criteria which may be required to standardize comparisons of statistics that are based on gonad indices.

Our results are conservative in the following respect. We have no knowledge of the frequency of spawning of female swordfish. Thus, because hydration of eggs may occur over a very short period of time, by not including individuals in class 4 ("mature ovaries" of Taylor and Murphy [1992]), some individuals that might be expected to spawn within a short period of time, and thus presumably within the general area of capture, may be excluded from consideration. The question of whether to include these individuals as reproductively active could be addressed by conducting a study of spawning frequency of female swordfish based on the condition of yolk development in the eggs, as has been done for yellowfin tuna, *Thunnus albacares* (Schaefer, 1996). Alternatively, it may be possible to determine whether or not class-4 individuals should be included

by estimating the distribution of spawning using both a classification scheme that considers these individuals as reproductively active, and the classification developed herein, with subsequent testing by comparison of these distributions to other measures of spawning activity, such as distributions of larval fish or of male:female ratios.

Given the interval estimate for OV, and taking a conservative approach with respect to including individuals that are not reproductively active in estimates of the spatial and temporal distributions of spawning, we recommend that researchers requiring an estimate of the reproductive status of female swordfish adopt a method that classifies reproductively active female swordfish as those for which $GI = \ln(GW)/\ln(EFL) \geq 1.375$, the upper limit of the interval. When additional information becomes available, further analyses should be undertaken.

The need to develop species-specific classification methodologies has been clearly documented (de Vlaming et al., 1982). However, methods for species with similar characteristics and reproductive habits may be similar (Cayré and Laloë, 1986). Merrett (1970) found that for sailfish (*Istiophorus platypterus*); striped (*Tetrapturus audax*), blue (*T. nigricans*), and black (*T. indica*) marlin; and spearfish (*T. angustirostris*), changes in ovaries through oogenic cycles were similar in all species, as was the shape of the gonads (with the exception of the shape of the spearfish gonad, which was Y-shaped rather than bilaterally symmetrical). These changes are similar to those observed in swordfish (cf. Taylor and Murphy, 1992). Thus, while we concur with de Vlaming et al. (1982) and strongly recommend that classification methods be developed and validated for each species of billfish, we would speculate that results for these species would be comparable to those shown herein.

Acknowledgments

We thank Kurt M. Schaefer and George M. Watters for their helpful discussions of various aspects of this manuscript during its development. We also thank William H. Bayliff and Richard B. Deriso for reviewing this manuscript and for their useful suggestions for its improvement. Helpful remarks were also received from three anonymous reviewers.

Literature cited

Arocha, F., and D. W. Lee.
1993. Preliminary observations on sex ratio and maturity stages of the swordfish, *Xiphias gladius*, in the northwest Atlantic. Int. Comm. Conserv. Atl. Tunas, Coll. Vol. Sci. Pap. 40(1):425–432.
1995. The spawning of swordfish from the northwest Atlantic. Int. Comm. Conserv. Atl. Tunas, Coll. Vol. Sci. Pap. 44(3):179–186.

Arocha, F., D. W. Lee and J. R. Grubich.
1994. Observations on sex ratio, maturity stages, and fecundity estimates of the swordfish, *Xiphias gladius*, in the northwest Atlantic Ocean. Int. Comm. Conserv. Atl. Tunas, Coll. Vol. Sci. Pap. 42(1):309–318.

Cayré, P., and F. Laloë.
1986. Review of the gonad index (GI) and an introduction to the concept of its "critical value": application to the skipjack tuna *Katsuwonus pelamis* in the Atlantic Ocean. Mar. Biol. 90:345–351.

de Vlaming, V., G. Grossman, and F. Chapman.
1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A(1):31–39.

Gouveia, L., and J. Mejuto.
1994. Notes on biological and biometric data of the swordfish (*Xiphias gladius* L.) in areas off Maderia. Int. Comm. Conserv. Atl. Tunas, Coll. Vol. Sci. Pap. 42(1):274–280.

Hinton, M. G., and R. B. Deriso.
In press. Distribution and stock assessment of swordfish in the eastern Pacific Ocean from catch and effort data standardized using biological and environmental parameters. *In* I. Barrett (ed.), Proceedings of the international symposium on Pacific swordfish; Ensenada, B.C., Mexico, 1994. U.S. Dep. Commer., NOAA Tech. Rep. NMFS.

Kume, S., and J. Joseph.
1969. Size composition and sexual maturity of billfish caught by the Japanese longline fishery in the Pacific Ocean east of 130° W. Bull. Jpn. Far Seas Fish. Res. Lab. 2:115–162.

Merrett, N. R.
1970. Gonad development in billfish (Istiophoridae) from the Indian Ocean. J. Zool., Lond. 160:355–370.

Miyabe, N., and W. H. Bayliff.
1987. A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1971–1980. Inter-Am. Trop. Tuna Comm. Bull. 19(1):1–163.

Murphy, M. D., and R. G. Taylor.
1990. Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. Fish. Bull. 88:531–542.

Nakano, H., and W. H. Bayliff.
1992. A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1981–1987. Inter-Am. Trop. Tuna Comm. Bull. 20(5):184–355.

Schaefer, K. M.
1996. Spawning time, frequency, and batch fecundity of yellowfin tuna, *Thunnus albacares*, near Clipperton Atoll in the eastern Pacific Ocean. Fish. Bull. 94:98–112.

Shingu, C., P. K. Tomlinson, and C. L. Peterson.
1974. A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1967–1970. Inter-Am. Trop. Tuna Comm. Bull. 16(2):65–230.

Sosa-Nishizaki, O.
1990. A Study on the Swordfish *Xiphias gladius* Stocks in the Pacific Ocean. Ph.D. diss., Department of Fisheries, Faculty of Agriculture, Univ. Tokyo, Tokyo, 246 p.

Taylor, R. G., and M. D. Murphy.
1992. Reproductive biology of the swordfish *Xiphias gladius* in the Straits of Florida and adjacent waters. Fish. Bull. 90:809–816.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Persistent spatial and temporal abundance patterns for late-stage copepodites of *Centropages hamatus* (Copepoda: Calanoida) in the U.S. northeast continental shelf ecosystem

Joseph Kane

National Marine Fisheries Service, NOAA
28 Tarzwell Drive, Narragansett, Rhode Island 02882-1199
E-mail address: jkane@whsun1.wh.whoi.edu

Abstract.—The annual cycle of abundance and the monthly distributions of the copepod *Centropages hamatus* are described for U.S. northeast continental shelf waters from plankton samples collected approximately bimonthly from 1977 to 1987. The copepod was found distributed throughout the study area with a strong onshore–offshore abundance gradient. After its annual low, *C. hamatus* was found to increase in abundance slowly along the coast and to expand offshore following the northward progression of spring conditions. The highest monthly mean abundance estimates of *C. hamatus* were found on Georges Bank during the month of July. Distribution begins to constrict inshore following peak abundance periods.

Examination of environmental variables revealed that in general *Centropages hamatus* was prevalent when surface temperatures ranged from 12 to 17°C, when water-column chlorophyll levels were high, and where salinity was low on the shelf. The population in the Middle Atlantic Bight subarea declines sharply as water temperatures rise in summer and does not begin to recover until temperatures decline in the fall. In contrast, populations in the more northern regions decrease slowly from peak abundance and do not increase from their annual low until water temperatures rise in early spring. The pelagic population that survives through low abundance periods is concentrated in shoal or inshore (or both) waters where temperature is low and phytoplankton biomass high. There was no evidence from survey data that predation by ctenophores, chaetognaths, or the copepod *Centropages typicus* has a major effect on *C. hamatus* abundance.

Manuscript accepted 10 July 1996.
Fishery Bulletin 95:85–98 (1997).

The calanoid copepod *Centropages hamatus* (Lilljeborg, 1853) is one of the dominant members of the zooplankton assemblage found within North Atlantic shelf waters (Davis, 1987; Sherman et al., 1987). The species has a wide latitudinal range that is reported to be as far north as Labrador (Pinhey, 1926) and southward to coastal waters off Florida in the Gulf of Mexico (Marcus, 1989). It occurs primarily in sheltered, coastal, and shoal regions of the continental shelf. This omnivorous copepod produces subitaneous eggs during the breeding season and also can produce diapausal ones in response to an environmental trigger (Pertzova, 1974; Marcus, 1989). McLaren (1978) estimated that generation period is comparatively short, 21–25 days at 12-13°C, and describes *C. hamatus* as a highly productive and ecologically efficient component of the zooplankton community. Sherman et al. (1987) reported that it is a major prey item of larval, juvenile, and adult fish stocks within continental shelf waters.

The National Marine Fisheries Service has monitored the zooplankton populations of the U.S. northeast shelf ecosystem with broad-scale surveys since 1977 as part of the MARMAP (Marine Resources Monitoring, Assessment, and Prediction) program (Sherman, 1980). The resulting historical data set provides the information needed to form a baseline for detection of future changes to the ecosystem. Previous reports on the annual abundance cycle of *Centropages hamatus* within the ecosystem have been limited to specific areas or to comparatively short periods (or both) (Bigelow, 1926; Deevey, 1956, 1960; Judkins et al., 1980; Davis, 1987; Sherman et al., 1987; Grant, 1988; Kane, 1993). No description of the monthly distribution of the copepod in this region has been published from collected data. This report uses information collected during MARMAP surveys from 1977 to 1987 to describe the persistent distribution and abundance patterns of *C. hamatus* throughout the ecosystem. Measurements of salinity, temperature, bottom depth, chlorophyll, and potential predator abundance were considered to gain insight into factors affecting the distribution and annual abundance cycle of *C. hamatus*.

Methods

Sample collection and analysis

The U.S. northeast shelf ecosystem extends from the Gulf of Maine to

Cape Hatteras (Sherman, 1994). Plankton samples were collected within the ecosystem at monthly or bimonthly intervals from 1977 to 1987. Plankton surveys occupied approximately 184 standard station locations that were relatively unchanged during the 11-yr period (Fig. 1). Samples were also collected on trawl and dredge cruises at randomly selected locations that varied yearly. Areal coverage and station spacing on these surveys were similar to broadscale plankton cruises.

Figure 1

Locations of standard MARMAP stations (•) in the U.S. northeast shelf ecosystem and subarea boundaries (MAB=Middle Atlantic Bight; SNE=Southern New England; GBK=Georges Bank; and GOM=Gulf of Maine).

Zooplankton were collected at each station from one side of a 61-cm bongo frame fitted with a 0.333-mm mesh net. The gear was lowered at 50 m/min to within 5 m of the bottom, or to a depth of 200 m maximum, and retrieved at 20 m/min. Ship speed was adjusted to maintain a 45° angle to the towing wire. A digital flowmeter was positioned in the center of the bongo frame to measure the volume of water filtered. All collections were preserved in 5% formalin. Samples were reduced to approximately 500 organisms in the laboratory by subsampling with a modified box splitter. Zooplankton were sorted, identified, and counted at the Plankton Sorting Center, Szczecin, Poland. The total number of samples analyzed for this report was 10,715. The abundance of *Centropages hamatus* is expressed here as numbers/100 m^3 of water filtered and includes only advanced copepodite stages CV and CVI. Earlier copepodite stages were excluded because other copepods of similar size are undersampled by 0.333-mm mesh nets (Anderson and Warren, 1991).

The seasonal abundance cycles of known predators of copepods captured with the nets used during the surveys were examined to determine which might affect *Centropages hamatus* population levels. The three copepod predators examined in this study are: 1) ctenophores, 2) the copepod *Centropages typicus*, and 3) chaetognaths.

Sea-surface temperature was measured at each station to the nearest 0.1°C with a stem thermometer. During plankton surveys from 1977 to 1986, water bottles with reversing thermometers were used to collect water samples at standard depths in order to measure salinity and temperature. Measurements of bottom temperature were determined by means of the deepest bottle or by means of a special bottom-tripped water-bottle sampler in water less than 75 m. Temperature and salinity data in 1987 were collected with a CTD (conductivity-temperature-depth) probe. Phytoplankton biomass was determined by measuring the concentration of chlorophyll *a* in the netplankton (>20 µmm) and the nanoplankton (<20 µmm) size fractions from water samples down to 100 m on plankton surveys from 1977 to 1984. These size fractions were summed to generate an estimate of total chlorophyll. The average water-column value of a variable for each station was calculated by arithmetically integrating measurements over depth.

More detailed accounts of sampling procedures and individual cruise tracks are given by Sibunka and Silverman (1984, 1989).

Statistical analysis

Estimates of *Centropages hamatus* and predator abundance were log transformed [$\log^{10}$(no./100m^3 +1)] prior to contouring and data analysis. Contoured *C. hamatus* distribution maps were made by using Surface III software (Sampson, 1988) on station abundance data from the 11-yr data set grouped by monthly intervals.

Evaluation of species interannual abundance variability was facilitated by subdividing the ecosystem into four subareas: Middle Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GBK), and Gulf of Maine (GOM) (Fig. 1). Each subarea is characterized by distinct patterns of circulation and bathymetry (Sherman et al., 1983). The average annual cycle of abundance and its variation was portrayed for each subarea by plotting the monthly mean abundance of all samples with its 95% confidence interval bar. Individual survey mean abundance and its 95% confidence interval bar were then superimposed on the latter plot. Surveys where the error bar did not overlap the one from the average cycle were judged to be situations where abundance departed substantially from the average cycle. Only surveys, except the one noted below, that covered 75% or more of a subarea were included in the analysis of interannual variability. Statistical analyses, comparing individual survey means with the time series monthly mean were not undertaken because they require the assumption of independence.

Several surveys (see Table 1) prior to 1981 were conducted by foreign vessels that did not have permission to sample east of the U.S.-Canada maritime boundary line in the GBK and GOM subareas. Although areal coverage in these surveys was reduced approximately 40% in relation to complete surveys, I included them in the analysis of this study because the area undersampled was consistent and our surveys still provided adequate coverage of the depth strata found within the two subareas.

Spearman's rank correlation coefficients were calculated for monthly subsets of station data to measure the strength of the relationship within individual months between *Centropages hamatus* abundance and the following variables: surface temperature, bottom depth, and the average water-column values of temperature, salinity, and total chlorophyll. Initial distribution plots of *C. hamatus* revealed that species abundance has a strong onshore–offshore gradient. Thus, to control the effect of depth on the calculation, Spearman's partial correlation coefficients were calculated for monthly subsets where both abundance and the other variable were significantly ($P<0.05$) correlated to depth.

Results

Distribution and abundance

The time-series mean distribution charts by month for *Centropages hamatus* are presented in Figure 2, A and B. Immediately apparent is the persistent onshore–offshore abundance gradient throughout the study area. There are high concentrations of the copepod inshore and within the shoal waters of GBK. Abundance in offshore waters is always much lower. *Centropages hamatus* is found throughout most of the ecosystem at some time during the year, the only exception being certain areas of the eastern offshore waters of the GOM where it is absent year round.

The timing of the annual abundance cycle of *Centropages hamatus* was not consistent throughout the ecosystem. The population in southern reaches of the study area declines through the summer, nearly disappearing from the water column during early autumn (Fig. 3). In December dense concentrations of *C. hamatus* begin to appear close to shore in the MAB subarea. These inshore centers of abundance slowly enlarge and expand along the coast and over the central shoals of GBK with the northward progression of spring (Fig. 2, A and B). Thus, peak times of abundance in the designated subareas vary with latitude (Fig. 3): May in the MAB, June in SNE, July on GBK, and September in the GOM. The population becomes distributed over nearly the entire shelf of each subarea during the annual peak period of abundance. The distribution and monthly abundance figures clearly show that GBK is the area of highest abundance for *C. hamatus* within the northeast shelf ecosystem.

Distribution begins to constrict towards the shore in each subarea during the months approaching the annual period of low abundance (Fig. 2). Abundance estimates in the SNE, GBK, and GOM subareas decline slowly through the autumn and, unlike the MAB region, do not reach the annual low until winter (Fig. 3).

Interannual variation in abundance of *Centropages hamatus* is shown in Figure 4 and individual survey statistics are given in Table 1. Although no long-term temporal trends in abundance were evident within any of the subareas, population estimates in certain years were exceptional. For example, the copepod's abundance in both the MAB and SNE subareas was high for an extended period in 1984 (Fig. 4). Both of these areas also had high abundance during the spring of 1987 and low population estimates in 1982. Departures from the average annual cycle of abundance were not always continuous across these subareas; *C. hamatus* density was low during early

Table 1

Centropages hamatus abundance data for each subarea by survey. The asterisk indicates where survey operations were not completed past the US-Canadian maritime boundary. Abbreviation Key: MAB = Middle Atlantic Bight; GBK = Georges Bank; SNE = Southern New England; GOM = Gulf of Maine; Yr = year; no. = number of samples, Mid-day = survey midpoint (jday), Log mean =log (10) mean abundance, SE = standard error of the mean.

MAB					SNE					GBK					GOM				
Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE
77	30	86	2.59	0.33	77	29	74	1.95	0.29	77	19	49	0.16	0.11	77	30	123	0.00	0.00
77	30	140	2.90	0.32	77	46	133	1.89	0.24	77	32	80	0.46	0.15	77	25	308	0.87	0.24
77	30	238	0.16	0.11	77	36	242	1.29	0.27	77	23	114	1.71	0.30	77	27	315	0.18	0.12
77	30	293	0.09	0.09	77	30	300	1.34	0.25	77	31	147	1.18	0.28	78*	25	139	0.09	0.09
78	29	49	1.16	0.27	78	31	60	1.07	0.20	77*	24	219	3.38	0.25	78*	31	193	0.44	0.17
78	28	112	2.00	0.29	78	30	131	1.38	0.25	77	19	307	2.58	0.45	78	29	240	0.46	0.18
78	29	177	2.43	0.30	78	34	188	2.12	0.27	77	22	333	2.47	0.32	78*	31	286	1.49	0.23
78	31	227	0.72	0.25	78	31	233	1.25	0.25	78	28	49	1.33	0.20	78*	31	322	0.44	0.17
79	46	59	1.74	0.24	78	31	294	1.62	0.28	78	29	137	0.46	0.19	79	40	114	0.06	0.06
79	30	129	3.06	0.29	79	40	64	1.64	0.20	78	19	241	3.04	0.42	79	32	147	0.19	0.11
79	49	172	2.74	0.22	79	27	107	1.12	0.29	78	32	287	2.84	0.25	79*	37	240	1.13	0.22
79	46	226	0.59	0.18	79	27	134	2.30	0.29	79	30	94	0.80	0.23	79	32	297	0.51	0.20
79	31	280	0.17	0.12	79	44	188	2.13	0.23	79	20	143	0.80	0.29	79	47	331	0.17	0.10
80	49	64	1.35	0.23	79	37	232	0.59	0.21	79*	18	192	2.38	0.50	80*	34	54	0.29	0.14
80	47	111	2.66	0.23	79	27	290	1.41	0.28	79*	17	238	3.15	0.43	80*	33	178	0.38	0.17
80	48	147	2.52	0.23	80	43	70	1.98	0.18	79	29	296	2.66	0.31	80*	37	217	1.06	.0.23
80	45	201	0.97	0.23	80	41	117	2.21	0.21	79	33	349	2.19	0.32	80	51	296	0.34	0.12
80	47	273	0.11	0.08	80	43	157	2.28	0.26	80*	20	62	1.49	0.35	81	53	52	0.13	0.07
80	40	327	0.66	0.22	80	40	207	2.56	0.22	80	29	88	1.32	0.30	81	46	146	0.44	0.14
81	48	82	1.82	0.24	80	43	282	0.38	0.15	80	28	123	1.46	0.34	81	40	339	0.19	0.11
81	43	90	2.08	0.30	80	44	341	1.08	0.23	80*	21	163	3.05	0.40	82	35	49	0.04	0.04
81	42	222	0.99	0.25	81	43	77	1.25	0.18	80*	20	215	3.13	0.36	82	48	124	0.13	0.08
81	43	271	0.00	0.00	81	44	103	1.39	0.23	80	30	293	1.68	0.33	82	37	156	0	0
82	35	80	1.75	0.27	81	35	162	2.07	0.25	80	30	353	1.49	0.29	82	49	302	0.50	0.17
82	44	81	2.60	0.26	81	33	191	2.75	0.29	81	26	66	0.29	0.14	82	52	334	0.44	0.15
82	29	157	1.62	0.31	81	30	228	1.80	0.35	81	20	96	0.92	0.30	83	53	26	0.25	0.09
82	34	214	1.29	0.28	81	38	284	1.43	0.26	81	24	115	1.63	0.32	83	38	116	0.46	0.13
82	38	268	0.55	0.19	82	40	75	1.62	0.19	81	24	157	1.57	0.40	83	55	167	0.68	0.15
83	36	53	1.33	0.28	82	34	100	1.25	0.25	81	31	196	3.34	0.32	83	46	306	0.22	0.11
83	39	78	2.05	0.27	82	44	146	1.44	0.21	81	52	296	2.36	0.25	83	31	349	0	0
83	46	149	2.60	0.18	82	39	198	2.58	0.20	81	32	335	1.71	0.32	84	47	14	0.20	0.10
83	33	212	0.31	0.13	82	24	285	1.86	0.38	82	29	64	0.47	0.18	84	40	112	0.20	0.12
83	43	268	0.07	0.07	82	43	348	1.20	0.21	82	36	109	1.22	0.22	84	54	151	0.36	0.11

continued on next page

spring 1979 in SNE (Fig. 4) and above average in the MAB (Table 1). There were no substantial upward abundance departures recorded on surveys of GBK and only one in the GOM (1978). This is probably due to the limited coverage the areas received during the peak periods of abundance (Fig. 4). There were several years in three of the subareas where survey mean abundance had substantial downward departures from the average annual cycle when *C. hamatus* was at or near its annual low (Fig. 4). These anomalies are probably not significant because log transformation increases the amplitude of low values. Plots of untransformed data show little interannual variation between survey means during low periods of abundance.

Correlation of abundance with other variables

Bottom depth *Centropages hamatus* abundance is negatively correlated to depth in all the subareas for most or all of the entire year (Table 2). Exceptions occur and correlations weaken during low periods of abundance in the MAB and GOM subareas when the copepod is present only at a few inshore locations.

Table 1 (continued)

MAB					SNE					GBK					GOM				
Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE
83	48	323	0.75	0.19	83	29	41	1.44	0.27	82	29	140	0.66	0.23	84	50	298	0.59	0.15
84	40	37	1.31	0.26	83	29	91	2.14	0.24	82	34	208	2.82	0.30	85	29	99	0.21	0.13
84	41	71	1.96	0.30	83	41	158	2.84	0.26	82	31	295	2.57	0.29	85	44	260	0.97	0.20
84	48	133	3.32	0.16	83	38	222	2.74	0.28	82	29	323	2.52	0.30	85	37	306	0.29	0.14
84	38	193	2.12	0.31	83	38	278	0.96	0.27	83	28	21	1.55	0.32	85	56	340	0.21	0.09
84	51	198	2.39	0.28	83	42	334	1.28	0.20	83	32	104	1.70	0.33	86	50	39	0.18	0.08
84	31	211	1.24	0.29	84	43	26	1.07	0.20	83	30	163	2.37	0.32	86	44	112	0.23	0.11
84	37	264	0.51	0.20	84	38	83	1.55	0.23	83	36	233	2.69	0.36	86	39	154	0.49	0.17
84	47	309	0.46	0.17	84	42	138	2.75	0.19	83	37	292	1.95	0.29	86	32	262	1.21	0.27
85	38	35	1.22	0.28	84	31	189	3.19	0.23	83	28	340	2.10	0.26	86	45	303	0.59	0.16
85	36	66	1.69	0.30	84	31	205	3.28	0.25	84	29	21	1.88	0.24	87	42	115	0.48	0.14
85	51	110	2.50	0.26	84	35	221	2.07	0.25	84	37	95	0.90	0.21	87	56	155	0.57	0.15
85	51	142	2.64	0.26	84	34	272	0.83	0.26	84	32	146	1.73	0.32	87	55	259	0.92	0.18
85	32	209	0.34	0.14	84	42	318	0.48	0.16	84	25	210	4.95	0.11	87	40	295	0.85	0.21
85	51	245	0.30	0.09	85	50	29	1.00	0.20	84	37	227	3.33	0.27					
85	26	277	0.17	0.12	85	29	79	1.57	0.27	84	35	284	2.37	0.28					
85	47	314	0.21	0.12	85	42	100	1.55	0.24	84	31	334	2.12	0.30					
86	46	12	0.60	0.18	85	43	137	1.93	0.26	85	31	14	2.08	0.25					
86	42	68	1.99	0.27	85	48	214	2.37	0.26	85	27	86	1.56	0.29					
86	46	133	2.37	0.29	85	44	254	1.32	0.24	85	31	94	1.20	0.29					
86	45	175	2.40	0.28	85	33	289	0.97	0.24	85	32	132	2.01	0.35					
86	41	217	0.73	0.20	85	42	323	0.79	0.18	85	45	235	2.78	0.29					
86	47	243	0.15	0.08	86	43	22	0.85	0.17	85	36	258	2.02	0.35					
86	40	263	0.06	0.06	86	31	88	2.41	0.27	85	32	297	1.76	0.34					
86	47	311	0.11	0.08	86	41	138	2.48	0.24	85	29	328	2.00	0.35					
87	47	10	1.45	0.24	86	31	189	2.88	0.31	86	31	35	2.17	0.28					
87	46	87	2.74	0.25	86	37	213	1.51	0.27	86	25	102	1.75	0.37					
87	51	105	3.53	0.15	86	42	252	1.29	0.24	86	31	150	1.95	0.30					
87	58	129	2.90	0.20	86	36	278	0.96	0.24	86	24	197	4.63	0.20					
87	29	193	1.27	0.31	86	43	316	1.56	0.23	86	36	237	3.70	0.23					
87	48	234	0.79	0.19	87	42	28	1.68	0.20	86	31	260	2.62	0.31					
87	37	261	0.27	0.11	87	37	100	2.45	0.24	86	26	293	2.14	0.32					
87	46	311	0.35	0.13	87	38	110	2.97	0.19	86	31	328	1.68	0.29					
					87	53	134	1.55	0.24	87	30	37	1.74	0.24					
					87	46	149	1.84	0.23	87	26	113	1.31	0.29					
					87	37	199	1.23	0.24	87	30	140	1.48	0.30					
					87	43	239	0.98	0.21	87	37	217	2.70	0.31					
					87	36	273	1.39	0.27	87	29	248	3.05	0.35					
					87	43	323	0.75	0.18	87	31	280	1.86	0.30					
										87	29	342	1.17	0.27					

Temperature *Centropages hamatus* was found at station locations where surface temperatures ranged from –0.5°C to 28.7°C and where the average water column temperatures were between 0.2 and 24.6°C. Although the copepod can tolerate a wide range of temperatures, abundance was greatest at stations where surface temperature ranged from 12 to 17°C (Fig. 5A).

The relationship between surface temperature and the annual abundance cycle is shown in Figure 3. Rising temperatures in the MAB during summer may be responsible for a rapid decline of *Centropages hamatus* there. The population nearly disappears during late summer as surface temperature reaches annual maximums. The July correlation coefficient between variables indicates a strong inverse relationship ($P<0.01$). *Centropages hamatus* density remains low until the mean surface temperature falls below 15°C in December. Abundance in the more northern subareas slowly declines after the annual temperature high is reached. Unlike that for the population in the MAB, abundance in these subareas does not increase as temperatures decline in the fall, but only with spring warming (Fig. 3).

Monthly correlations between *Centropages hamatus* station abundance and temperature variables

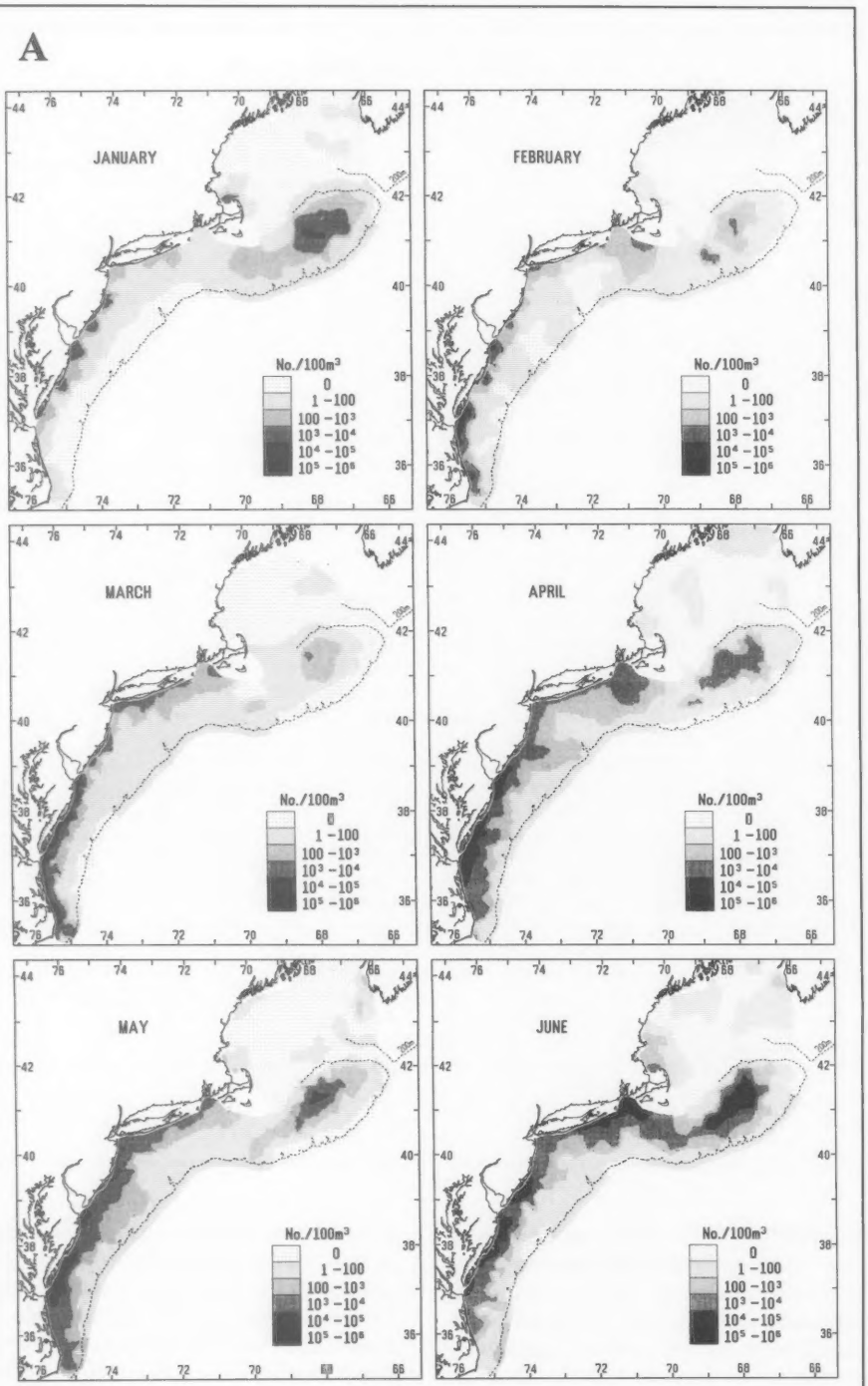


Figure 2

(A) Monthly composite distribution and abundance of *Centropages hamatus* in the U.S. northeast shelf ecosystem: 1977–1987. (B) Monthly composite distribution and abundance of *Centropages hamatus* in the U.S. northeast shelf ecosystem: 1977–1987.

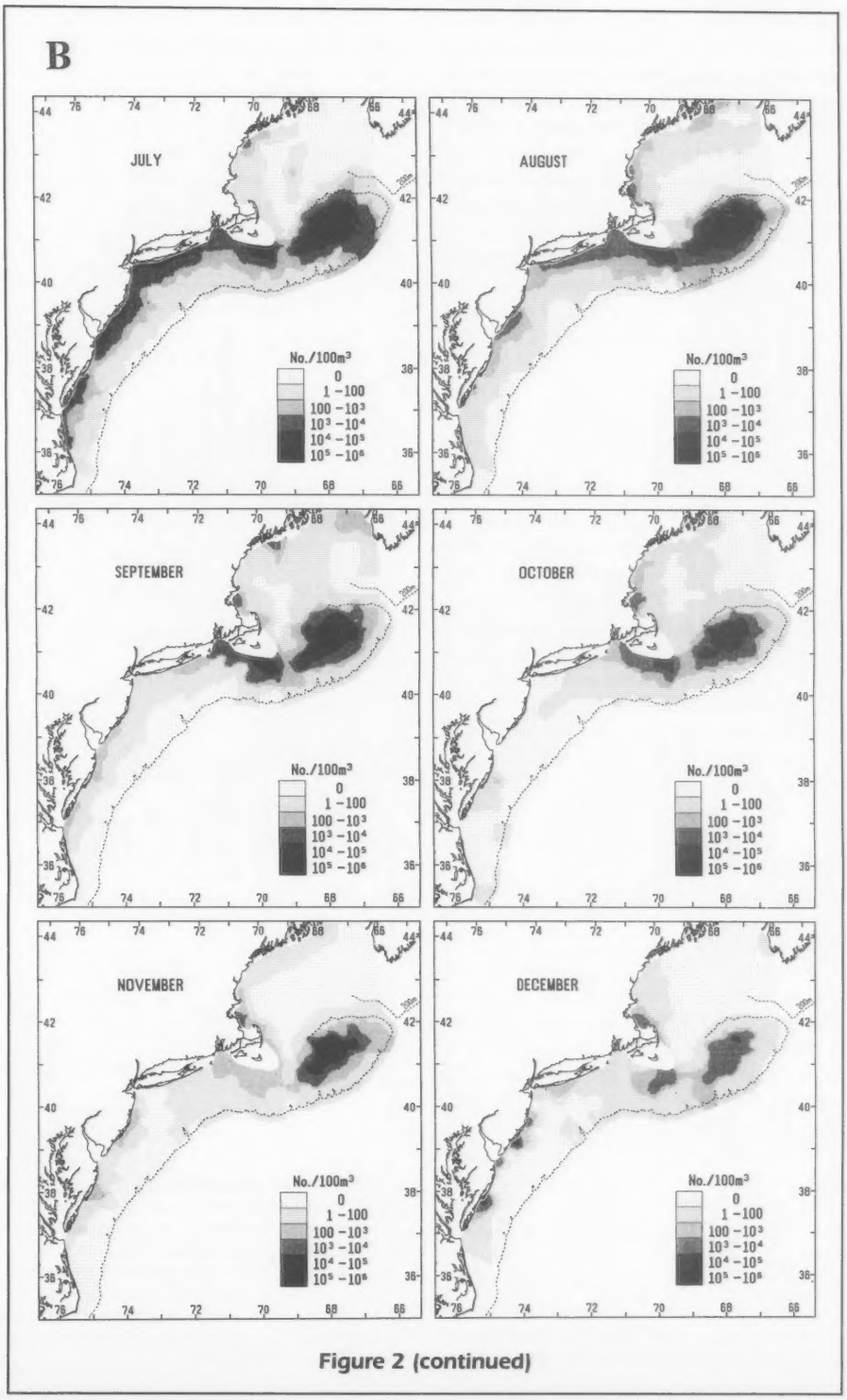


Figure 2 (continued)

were significant ($P<0.05$) during certain months in each of the subareas (Table 2). Significant relationships persisted between *C. hamatus* density and a temperature variable for several extended periods. Surface temperature was negatively correlated with abundance from November to March in the MAB subarea and also from June to February in SNE waters. Abundance in the GBK subarea was positively correlated to average water-column temperatures from May to July and with bottom temperatures from September to December. In the GOM sub-

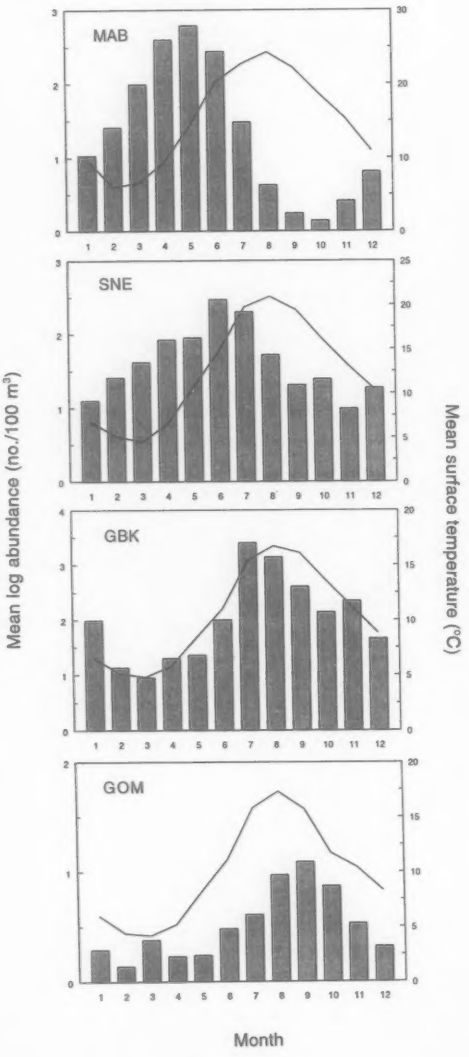


Figure 3

Bar graph of the monthly log mean abundance of *Centropages hamatus* with a line graph of the monthly mean surface water temperature for each subarea (MAB=Middle Atlantic Bight; SNE=Southern New England; GBK=Georges Bank; and GOM=Gulf of Maine) .

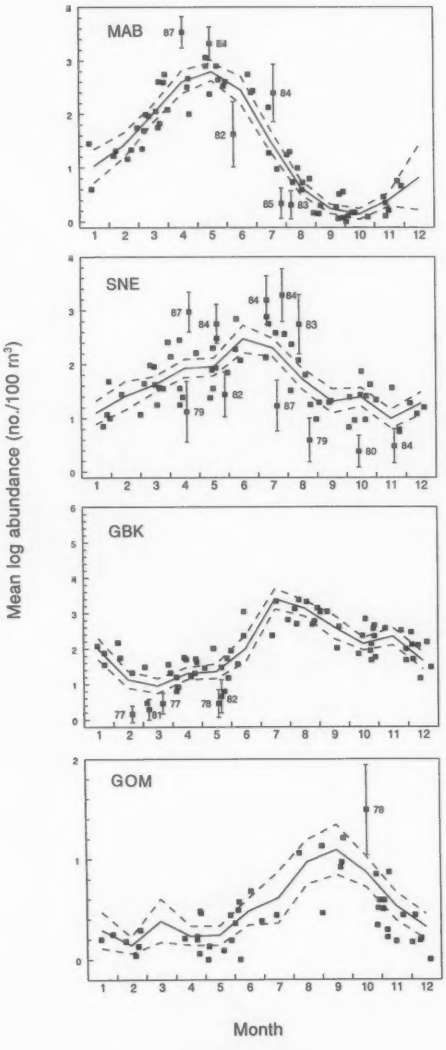


Figure 4

Time series monthly log mean abundance (solid line) of *Centropages hamatus* and the 95% confidence interval (dashed line) of the mean for each subarea. Single points are the log mean abundance of individual surveys. Surveys that departed substantially from the time series mean are labeled and the 95% confidence interval of the mean indicated with a error bar (MAB=Middle Atlantic Bight; SNE=Southern New England; GBK=Georges Bank; and GOM=Gulf of Maine).

area there were no strong correlations for extended periods between variables.

Chlorophyll Estimates of the abundance of *Centropages hamatus* were highest at locations where chlorophyll biomass was also high (Fig. 5B). Total chlorophyll and abundance measures at stations were significantly ($P<0.01$) correlated during certain times of the year in all subareas (Table 2). In the MAB, variables were positively correlated from May through July and, in SNE waters, during October and February. Variables on GBK were positively correlated from May through January, except for October. GOM correlations were significantly positive in August, November, and December.

Partitioning of total chlorophyll values into netplankton and nanoplankton size fractions did not typically change the correlation coefficients between *Centropages hamatus* and phytoplankton abundance listed in Table 2. There were a few scattered months in the subareas where coefficients with netplankton were 0.1–0.2 units higher. The most substantial change occurred during October on GBK. The correlation coefficient with netplankton was 0.27 units above the value in Table 2 and was positively correlated ($P=0.02$).

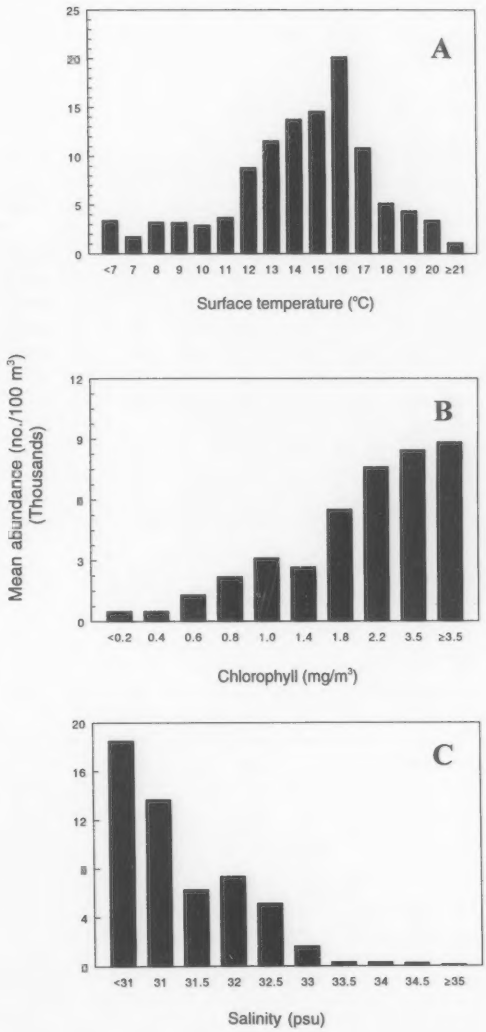


Figure 5

Mean abundance of *Centropages hamatus* by (**A**) surface temperature, (**B**) chlorophyll, and (**C**) salinity interval. All time series data from the entire survey area was used.

Salinity *Centropages hamatus* was present at stations where integrated water-column salinity ranged from 27.09 to 36.00 psu. Maximum abundance occurred in the lower region of this range (Fig. 5C). Monthly correlation coefficients between station abundance and salinity were usually negative and oftentimes significant during the year (Table 2). Notable were the comparatively high negative correlations found during January in both the MAB and SNE subareas. Values in the MAB were also negatively correlated in February and again in August and September. SNE correlations were also significantly negatively correlated during April, July, and from September through December. GBK correlations, though not always significant, were positive from February through July and negative in the remaining six months. GOM coefficients were generally weak throughout the year.

Predation Pressure On average, *Centropages hamatus* and ctenophores both reach peak abundance during June in the SNE subarea (Figs. 3 and 6). During June and July of 1981 a large patch (9–12 stations) of ctenophores occupied inshore waters in the southern region of the subarea offshore of Long Island, New York. This concentration pushed overall mean abundance in the subarea to an 11-year high (Fig. 6). Predation on *C. hamatus* was apparently minimal; its mean abundance in late spring 1981 was slightly above the 11-year average (Table 1; Fig. 3). However, the abundance of *C. hamatus* in June within a ctenophore patch was much lower (611/100m^3) than outside (2,712/100m^3) it. Evidence for predation pressure was also found in the July survey; *C. hamatus* density was 8,138/100m^3 where it cooccured with ctenophores, 22,871/100m^3 where ctenophores were absent.

In the SNE subarea, the omnivorous copepod *Centropages typicus* is present at relatively high lev-

Table 2

Summary of correlation analysis between abundance and the different environmental variables. An asterisk indicates where partial correlation coefficients were used. Abbreviation key: temp. = temperature; chl. = chlorophyll; no. = number of observations; r = spearman correlation coefficient; P = probability that correlation is zero; MAB = Middle Atlantic Bight; SNE = Southern New England; GBK = Georges Bank; GOM = Gulf of Maine.

		Bottom Depth			Surface temp.			Column temp.			Bottom temp.			Column salinity			Total chl.		
Area	Month	no.	r	P	no.	r	P	no.	r	P	no.	r	P	no.	r	P	no.	r	P
MAB	1	93	−0.54	<0.01	89	−0.45	<0.01*	93	−0.47	<0.01*	90	−0.48	<0.01*	93	−0.54	<0.01*	0		
	2	190	−0.63	<0.01	190	−0.23	<0.01*	145	−0.33	<0.01*	139	−0.33	<0.01*	146	−0.40	<0.01*	146	−0.01	0.89*
	3	434	−0.65	<0.01	432	−0.11	0.03*	148	0.05	0.55*	139	0.05	0.60*	148	−0.18	0.03*	161	0.16	0.04
	4	223	−0.65	<0.01	218	−0.02	0.77	67	0.12	0.35	66	0.05	0.68	67	0.09	0.45*	75	0.05	0.64
	5	352	−0.68	<0.01	350	0.01	0.82	278	−0.05	0.41*	266	−0.02	0.78*	278	−0.21	<0.01*	197	0.24	<0.01*
	6	162	−0.64	<0.01	161	−0.03	0.75	75	−0.12	0.29*	73	−0.12	0.31*	75	−0.17	0.16*	79	0.25	0.03*
	7	290	−0.50	<0.01	287	−0.42	<0.01*	19	0.30	0.23*	19	0.30	0.21	19	−0.41	0.09*	70	0.38	<0.01*
	8	354	−0.22	<0.01	352	−0.01	0.98*	146	−0.18	0.04*	143	−0.18	0.04*	146	−0.30	<0.01*	77	0.18	0.12*
	9	313	−0.20	<0.01	306	0.01	0.89	93	−0.09	0.37*	86	−0.24	0.03*	93	−0.28	<0.01*	38	0.20	0.24*
	10	128	−0.04	0.70	127	0.12	0.19	73	0.18	0.14	69	0.17	0.16	73	−0.04	0.76	80	−0.02	0.84
	11	278	−0.36	<0.01	278	−0.24	<0.01	266	−0.23	<0.01	257	−0.20	<0.01	266	−0.08	0.17*	117	0.08	0.38*
	12	27	−0.69	<0.01	27	−0.31	0.12*	26	−0.21	0.32*	25	−0.22	0.31*	26	−0.23	0.27*	27	−0.12	0.56*
SNE	1	146	−0.34	<0.01	146	−0.41	<0.01*	145	−0.44	<0.01*	132	−0.43	0.01*	145	−0.52	<0.01*	64	−0.29	0.02*
	2	92	−0.39	<0.01	92	−0.29	<0.01*	63	0.08	0.56*	57	0.02	0.90*	63	−0.03	0.82*	66	0.25	0.05*
	3	339	−0.33	<0.01	336	−0.01	0.98*	175	−0.11	0.14*	165	−0.09	0.27*	175	−0.09	0.22*	205	−0.04	0.59*
	4	314	−0.42	<0.01	282	0.07	0.24*	61	−0.35	<0.01*	56	−0.35	0.01*	61	−0.49	<0.01*	58	−0.23	0.09*
	5	371	−0.51	<0.01	365	0.08	0.15	245	0.14	0.03*	230	0.23	<0.01*	241	−0.02	0.81*	167	0.17	0.03*
	6	146	−0.56	<0.01	146	−0.30	<0.01*	119	−0.07	0.46	110	0.06	0.55	119	−0.16	0.08*	123	0.01	0.95*
	7	343	−0.66	<0.01	343	−0.27	<0.01*	66	0.22	0.08*	63	0.24	0.06	66	−0.34	<0.01*	107	−0.05	0.63*
	8	289	−0.32	<0.01	286	−0.36	<0.01	89	−0.01	0.90*	89	0.09	0.39*	89	−0.14	0.21*	68	0.09	0.48*
	9	188	−0.33	<0.01	176	−0.44	<0.01*	104	−0.28	<0.01*	101	0.14	0.18*	104	0.28	<0.01*	14	0.52	0.06
	10	354	−0.27	<0.01	327	−0.58	<0.01*	113	−0.33	<0.01*	106	0.10	0.34*	113	−0.24	<0.01*	133	0.20	0.02*
	11	225	−0.15	0.03	224	−0.36	<0.01*	205	−0.31	<0.01*	191	−0.22	<0.01	205	−0.14	0.05*	76	0.11	0.37*
	12	160	−0.22	<0.01	158	−0.22	<0.01*	146	−0.16	0.06*	139	−0.02	0.78*	146	−0.37	<0.01*	141	0.01	0.91*
GBK	1	100	−0.69	<0.01	100	−0.14	0.17	71	0.24	0.05*	61	0.24	0.07*	71	−0.04	0.77*	72	0.28	0.02*
	2	104	−0.42	<0.01	103	0.38	<0.01*	54	0.52	<0.01*	45	0.50	<0.01*	54	0.24	0.08*	12	0	0
	3	152	-0.51	<0.01	148	0.03	0.70*	75	0.01	0.92*	66	−0.16	0.21	75	0.22	0.06*	92	−0.10	0.34*
	4	292	−0.53	<0.01	287	0.13	0.03	53	0.19	0.18*	46	0.22	0.15*	53	0.23	0.10*	28	0.31	0.10
	5	250	−0.61	<0.01	241	0.16	<0.01*	171	0.33	<0.01	153	0.30	<0.01	171	0.27	<0.01*	134	0.45	<0.01*
	6	97	−0.64	<0.01	93	−0.02	0.88*	69	0.40	<0.01*	58	0.45	<0.01*	69	0.14	0.26*	63	0.30	0.02*
	7	163	−0.64	<0.01	161	−0.29	<0.01*	31	0.47	<0.01*	30	0.37	0.05*	31	0.18	0.35*	42	0.36	0.02*
	8	250	−0.67	<0.01	242	−0.19	<0.01*	28	0.04	0.83*	25	0.03	0.91*	28	−0.55	<0.01*	48	0.33	0.03*
	9	124	−0.73	<0.01	108	−0.21	0.03	96	0.19	0.07*	87	0.33	<0.01*	96	−0.16	0.12*	23	0.47	0.03*
	10	393	−0.62	<0.01	388	0.21	<0.01	63	0.12	0.37*	55	0.42	<0.01*	63	−0.41	<0.01*	78	−0.01	0.99*
	11	194	−0.73	<0.01	194	0.11	0.14*	151	0.09	0.29	138	0.21	<0.01	151	−0.13	0.13*	94	0.21	0.04*
	12	165	−0.62	<0.01	152	0.36	<0.01	135	0.31	<0.01	114	0.30	<0.01	135	−0.12	0.16*	95	0.38	<0.01*
GOM	1	95	−0.12	0.26	95	0.01	0.95	59	−0.05	0.70	42	−0.13	0.40	59	−0.06	0.65	8	−0.25	0.55
	2	204	−0.23	<0.01	193	−0.01	0.95*	136	−0.04	0.62*	79	−0.05	0.64*	136	0.06	0.49*	99	0.18	0.07*
	3	70	−0.24	0.05	70	0.06	0.64	48	0.04	0.81	29	−0.05	0.80	48	−0.01	0.96	63	0.12	0.35
	4	288	−0.10	0.08	257	−0.01	0.97	19	−0.13	0.58	10	−0.12	0.74	19	−0.26	0.28	17	−0.22	0.40
	5	278	−0.22	<0.01	251	0.04	0.52*	136	0.17	0.54	84	0.36	<0.01*	136	0.06	0.46*	113	−0.01	0.91*
	6	245	−0.35	<0.01	244	0.10	0.11	189	0.10	0.17	105	−0.31	<0.01	149	−0.13	0.11*	52	−0.16	0.25
	7	75	−0.19	0.10	74	0.07	0.54	37	0.07	0.69	30	0.06	0.75	37	−0.11	0.52	45	0.19	0.20
	8	172	−0.40	<0.01	162	−0.06	0.45*	48	0.25	0.09*	46	0.21	0.17	48	−0.22	0.14*	93	0.25	0.01*
	9	155	−0.28	<0.01	145	<0.01	0.99*	135	−0.09	0.29*	114	−0.20	0.03*	135	−0.12	0.16*	23	−0.06	0.80
	10	307	−0.18	<0.01	302	0.10	0.09*	100	−0.01	0.89*	54	−0.02	0.91*	100	−0.15	0.13*	118	0.08	0.40
	11	274	−0.42	<0.01	272	0.18	0.01*	93	0.20	0.06*	65	0.10	0.42*	93	−0.27	<0.01*	93	0.29	<0.01
	12	274	−0.29	<0.01	269	0.05	0.42*	251	0.05	0.44	167	−0.07	0.38*	251	−0.02	0.72*	107	0.24	0.01

els year round and begins to increase inshore from its annual low in late spring-early summer (Fig. 6) when *Centropages hamatus* is at peak abundance. MARMAP data indicate that it is unlikely that the summer decline or the abundance levels reached by *C. hamatus* are controlled substantially by *C. typicus* predation. There was no strong inverse relationship between the abundance trends of the two species. For example, in 1987 *C. hamatus* reached peak abundance earlier than usual, in late April, and declined rapidly to below average levels (Table 1). The abundance of *C. typicus* was average in late April 1987 and also declined through the summer to below average levels (Fig. 6). High levels of *C. hamatus* recorded in 1984 (Fig. 4) were not due to the absence of *C. typicus* predators; abundance was close to average for the copepod during spring and summer (Fig. 6). Monthly partial correlation coefficients between station abundance values of the two species during the time series were positive (0.07–0.24) from April through August, further evidence that predation by *C. typicus* is minimal.

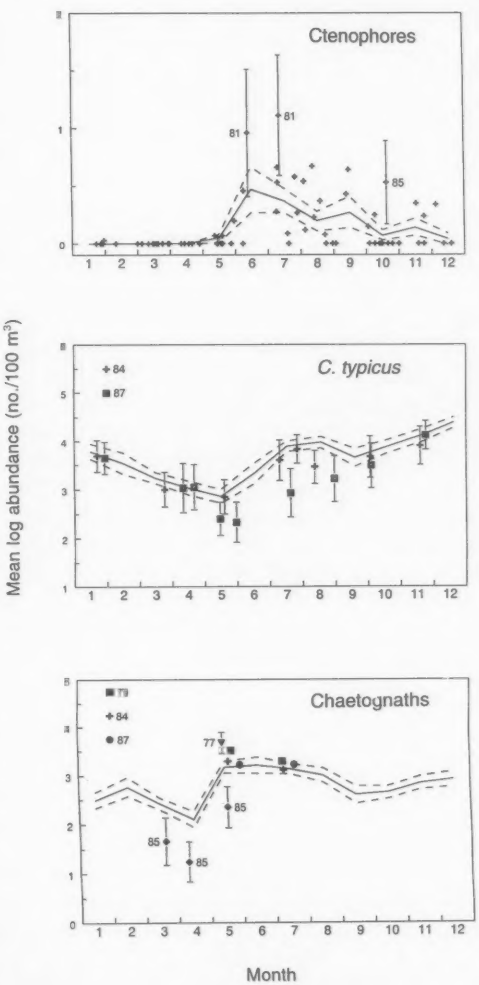


Figure 6

Time series monthly log mean abundance (solid line) and the 95% confidence interval (dashed line) of the mean for the following copepod predators in the Southern New England subarea: ctenophores, the copepod *Centropages typicus*, and chaetognaths. Single points are the log mean abundance of the taxon for individual surveys during certain years. The error bars indicate the 95% confidence interval of the mean.

Peaks of *Centropages hamatus* abundance and the presence of chaetognaths do coincide in the SNE subarea (Figs. 3 and 6). However, evidence that chaetognathan predation impacts *C. hamatus* abundance could not be found. All of the surveys that had exceptional high or low *C. hamatus* abundance, 1979, 1984, and 1987 (Fig. 4), had near average chaetognath density (Fig. 6). Conversely, *C. hamatus* abundance was close to average when chaetognath density was high in 1977 and low in 1985 (Fig. 6). Monthly partial correlation coefficients between station abundance values of the two species were not significant and very low (–0.10–0.25) throughout the year, indicating that chaetognath predation has little effect on *C. hamatus* abundance.

Discussion

Temperature affects most processes in marine ecosystems and the life cycle of *Centropages hamatus* is no exception. Opposite extremes in temperature appear to limit the seasonal occurrence of the population at the southern and northern ends of the ecosystem. Warm summer temperatures in the MAB were correlated with the rapid decline of the copepod in this area as values approach or surpass the critical upper thermal level for the species. Similar relationships between temperature and *C. hamatus* were found by Deevey (1960) for the population present near and within Delaware Bay. She reported that the copepod disappears as temperatures rise in summer but is present year round in small numbers during cool summers. Grant (1988) also reported that *C. hamatus* abundance in the MAB declines with increasing temperature and is absent in some years during summer and fall seasons. The MAB population begins to reappear or increase close inshore in late autumn where waters cool faster than those offshore. Populations farther north decline slowly as

winter approaches until only small aggregations of cold-adapted individuals overwinter in the far eastern waters along the SNE coast, on the central shoals of GBK, and within inshore waters in the GOM. Abundance in these areas increase as temperatures rise in spring.

The life cycle of many marine copepods involves the production of resting eggs that allow the species to repopulate areas when environmental conditions again become favorable (Uye, 1985). Evidence that *Centropages hamatus* produce resting eggs has been found in the western North Atlantic (Lindley, 1990), the Gulf coast of Florida (Marcus, 1989), and in the MARMAP survey area on GBK (Davis, 1987). Although this report provides no direct evidence that *C. hamatus* produces resting eggs, it seems unlikely that the small pelagic population that overwinters, or oversummers, could produce the great abundance of the next generation without recruitment from benthic resting eggs. Marcus (1989) found that a *C. hamatus* population residing in a subtropical embayment area produces diapause eggs that allow the species to survive warm summer temperatures. This also likely occurs in the MAB when the population rapidly declines to a few individuals, or disappears entirely during summer, and begins to increase as temperatures decline in winter. Lower maximum temperatures observed on GBK are apparently not sufficiently high to impact populations there dramatically; abundance declines slowly during autumn after peak abundance is reached in summer and does not increase until temperatures rise in early spring. This slow decline in abundance may occur because success of egg hatching decreases as females gradually switch from subitaneous egg production to resting egg production owing to decreasing temperatures and daylengths, as was found for the copepod *Labidocera aestiva* in nearby waters (Marcus, 1982). The resting eggs hatch in the spring to supplement the production of overwintering late-stage copepodites and to ensure the success of the population. Such variation in egg production between well-separated populations has been reported for other species (Marcus, 1984; Uye, 1985). Somewhere in the SNE subarea there is probably a transition zone between adults that are "temperature shocked" to release quiescent eggs and those that slowly change their egg-laying strategy as autumn progresses. Egg-production strategy in the GOM is probably similar to that found in the GBK.

The strongly negative correlation of *Centropages hamatus* abundance to depth and its well-defined inshore–offshore abundance gradient confirm the importance of resting eggs in the life history of this species. Environmental conditions probably do not trigger the release of diapause eggs until after the population constricts inshore after peak abundance is reached. Evidence for this was found by Lindley (1990) in southern waters of Great Britain where *C. hamatus* eggs were found to be abundant only in depths of less than 50 m. When the eggs hatch, the prevailing westerly winds in the northwest Atlantic slowly spread the pelagic population and the new recruits offshore to establish the characteristic abundance gradient of this species.

Abundance of *Centropages hamatus* appears to be related strongly to the availability of phytoplankton. The copepod's abundance was highest at stations where chlorophyll values were high, and its distribution is similar to phytoplankton gradients in the study area (O'Reilly and Busch, 1984). However, correlation coefficients between variables were weak and inconsistent among subareas, indicating that the species is not particularly sensitive to phytoplankton availability. The low correlation may be because average water-column chlorophyll measurements are static measures that may not reflect the actual food concentrations that are, or were, available to the copepod over the previous 24 hours. Furthermore, it is also possible that late-stage copepodites of this omnivorous species may be more sensitive to zooplankton prey concentrations. Nonetheless, food availability is a key limiting factor throughout nature and certainly has a major role in shaping the life history of this copepod. The maximum mean abundance of *C. hamatus* is greatest on GBK, the ecosystem subarea with the largest estimate of annual primary production (O'Reilly et al., 1987). Conversely, population density is lowest in the GOM where average chlorophyll concentrations are also lowest.

Monthly correlation coefficients between salinity and abundance of *Centropages hamatus* were also weak even though both variables have a strong offshore gradient. Unlike chlorophyll correlations, these coefficients portray accurately the relationship between variables. *Centropages hamatus* is a coastal species with a wide latitudinal range and must tolerate wide environmental fluctuations. It has been reported in areas with salinity as low as 6 psu (Hernroth and Ackefors, 1977), as well as in Mediterranean waters where salinity exceeds 36 psu (Gaudy, 1971). The large numbers of *C. hamatus* associated with low salinity found in this study is probably an artifact of the high phytoplankton concentrations found in a narrow inshore band along the MAB and SNE coasts (O'Reilly et al., 1987). The annual spring increase in precipitation and subsequent river runoff that leads to lowered salinity in the MAB and SNE subareas (Manning, 1991) also introduces nutrient-enriched water that stimulates phytoplankton growth and zooplankton production. Further-

more, the highest mean abundance of *C. hamatus* is found over the central shoals of GBK where salinity usually ranges from 32.2 to 32.7 psu during peak abundance, well above the coastal areas where abundance, on average, is much lower. High salinity offshore may effect *C. hamatus* production there and restrict its distribution, but it is more likely that low offshore abundances are caused by low phytoplankton food stocks that cannot support an overwintering population or the generation that produces resting eggs after peak abundance is reached.

There was no strong evidence from survey data that predation affects interannual variability or causes the seasonal decline of the population in the SNE subarea. Ctenophores appear to lower *Centropages hamatus* abundance when they are plentiful, but this occurred only during one year and in a restricted area. Chaetognaths and the copepod *Centropages typicus* also appear to have little affect on *C. hamatus* density. Clearly, however, a dedicated study analyzing stomach contents and the vertical distribution of the predator-prey field is needed to define the actual food web. Potential predators such as squid, juvenile fish, and populations of planktiverous adult fish must also be considered in order to fully define the role predation has in controlling *C. hamatus* population levels.

Lindley and Hunt (1989) examined the distribution of *Centropages hamatus* to the north and across the Atlantic to the North Sea. They described a life cycle similar to the one reported in this paper and speculated that the autumn decline in abundance is caused by the pressure of competition with *Centropages typicus* for food resources. Dagg and Turner (1982) studied copepod populations in the SNE and GBK subareas during autumn and calculated that copepod grazers may consume entire phytoplankton stocks. If true, high abundance of *C. typicus* could impact population levels of *C. hamatus*. However, MARMAP survey data indicate that high *C. typicus* abundance does not lead to an early decline of *C. hamatus* in either subarea. For example, in 1985 on GBK, median *C. typicus* abundance was 2–3 orders of magnitude above the ten-year average, but *C. hamatus* was also above average and increased in late autumn (Kane, 1993). Data presented in this report also show that the abundance of the two species are not related in the SNE subarea. Although competition pressure between the two species does not appear to cause the decline of *C. hamatus*, laboratory feeding experiments are needed to measure the effect of low food levels on species abundance.

The copepod *Centropages hamatus* has evolved a unique life history to survive and reproduce within the waters of the northwestern Atlantic continental shelf. The population has a distinct seasonal cycle with peak abundance occurring in shallow areas where phytoplankton food stocks are rich and surface temperature ranges from 12 to 17°C. Predation pressure appears minimal, and *C. hamatus* abundance peaks between the annual maximum of early spring and autumn dominant copepod species (Sherman et al., 1983), thus reducing competition pressure for food resources. *Centropages hamatus* likely produces resting eggs that hatch and help repopulate the ecosystem when environmental conditions are favorable. Comprehensive laboratory and shipboard experiments are needed to distinguish how the above biotic and abiotic factors interact to determine the annual success of the population.

Acknowledgments

The author acknowledges the individuals involved with the collection, analysis, and processing of MARMAP data. Special thanks go to Jay O'Reilly for his help with the distribution plots and to those who critically reviewed early drafts of the manuscript.

Literature cited

Anderson, J. T., and W. G. Warren.
1991. Comparison of catch rates among small and large bongo samplers for *Calanus finmarchicus* copepodite stages. Can. J. Fish. Aquat. Sci. 48:303–308.

Bigelow, H. B.
1926. Plankton of the offshore waters of the Gulf of Maine. Bull. of the Bureau of Fish. XL, part 2. Gov't Printing Office, Washington D.C., 509 p.

Dagg, M. J., and J. T. Turner.
1982. The impact of copepod grazing on the phytoplankton of Georges Bank and the New York Bight. Can. J. Fish. Aquat. Sci. 39:979–990.

Davis, C. S.
1987. Zooplankton life cycles. *In* R. A.Bakus and D. W. Bourne (eds.), Georges Bank, p. 256–267. MIT Press, Cambridge, MA.

Deevey, G. B.
1956. Oceanography of Long Island Sound, 1952–1954. Bull. Bingham Oceanogr. Collect., Yale Univ. 15:113–155.
1960. The zooplankton of the surface waters of the Delaware Bay region. Bull. Bingham Oceanogr. Collect., Yale Univ. 17(2):5–53.

Gaudy, R.
1971. Contribution a l'étude du cycle biologique des copepodes pelagiques du Golf de Marseille. I: L'environment physique et biotique et la composition de la population de copepodes. Tethys 3(4):921–942.

Grant, G. C.
1988. Seasonal occurrence and dominance of *Centropages* congeners in the Middle Atlantic Bight, USA. Hydrobiol. 167/168:227–237.

Hernroth, L., and H. Ackefors.
1977. The zooplankton of the Baltic proper: a long term investigation of the fauna, its biology and ecology. Institute of Mar. Res., Lysekil, Sweden, 58 p.

Judkins, D. C., C. D. Wirick, and W. E. Esaias.
1980. Composition, abundance, and distribution of zooplankton in the New York Bight, September 1974–September 1975. Fish. Bull. 77:669–683.

Kane, J.
1993. Variability of zooplankton biomass and dominant species abundance on Georges Bank, 1977–1986. Fish. Bull. 91(3):464–474.

Lindley, J. A.
1990. Distribution of overwintering calanoid copepod eggs in sea-bed sediments around southern Britain. Mar. Biol. 104:209–217.

Lindley, J. A., and H. G. Hunt.
1989. The distributions of *Labidocera wollastoni* and *Centropages hamatus* in the north Atlantic Ocean and the North Sea in relation to the role of resting eggs in the sediment. *In* J. S. Ryland and P. A. Tyler (eds.), Reproduction, genetics, and distribution of marine organisms, p. 407–413. Olson and Olson Press, Fredensborg, Denmark.

Manning, J.
1991. Middle Atlantic Bight salinity: interannual variability. Continental Shelf Res. 11(2):123–137.

Marcus, N. H.
1982. Photoperiodic and temperature regulation of diapause in *Labidocera aestiva* (Copepoda: Calanoida). Biol. Bull. 162:45–52.
1984. Variation in the diapause response of *Labidocera aestiva* (Copepoda: Calanoida) from different latitudes and its importance in the evolutionary process. Biol. Bull. 166:127–139.
1989. Abundance in bottom sediments and hatching requirements of eggs of *Centropages hamatus* (Copepoda: Calanoida) from the Alligator Harbor region, Florida. Biol. Bull. 176:142–146.

McLaren, I. A.
1978. Generation lengths of some temperate marine copepods: estimation, prediction, and implications. J. Fish. Res. Board Can. 35:1330–1342.

O'Reilly, J. E., and D. A. Busch.
1984. Phytoplankton primary production on the northwestern Atlantic shelf. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 183:255–268.

O'Reilly, J. E., C. Evans-Zeitland, and D. A. Busch.
1987. Primary production. *In* R. A. Bakus and D. W. Bourne (eds.), Georges Bank, p. 220–233. MIT Press, Cambridge, MA.

Pertzova, N. M.
1974. Life cycle and ecology of a thermophilous copepod *Centropages hamatus* in the White Sea. Zool. Zh. 52:1013–1022.

Pinhey, K.
1926. Entomostraca of the Belle Isle Strait expedition, 1926, with notes on other planktonic species, part I. Contrib. Can. Biol., N.S. 3:1–55.

Sampson, R. J.
1988. SURFACE III users manual. Kansas Geological Survey, Lawrence, KS, 277 p.

Sherman, K.
1980. MARMAP, a fisheries ecosystem study in the NW Atlantic: fluctuations in the ichthyoplankton–zooplankton components and their potential for impact on the system. *In* F. P.Diemer, F. J. Vernberg, and D. Z. Mirkes, (eds.), Advanced concepts on ocean measurements for marine biology, p. 9–37. Belle W. Baruch Institute for Marine Biology and Coastal Res., Univ. South Carolina Press, Columbia, SC.
1994. Sustainability, biomass yields, and health of coastal ecosystems: an ecological perspective. Mar. Ecol. Prog. Ser. 112(3):277–301.

Sherman, K., J. R. Green, J. R. Goulet, and L. Ejsymont.
1983. Coherence in zooplankton of a large Northwest Atlantic ecosystem. Fish. Bull. 81(4):855–862.

Sherman, K., W. G. Smith, J. R. Green, E. B. Cohen, M. S. Berman, K. A. Marti, and J. R. Goulet.
1987. Zooplankton production and the fisheries of the Northeastern Shelf. *In* R. A. Bakus and D. W. Bourne (eds.), Georges Bank, p. 268–282. MIT Press, Cambridge, MA.

Sibunka, J. D., and M. J. Silverman.
1984. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1977–1983). Atlas No. 1: summary of operations. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-33.
1989. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1984-1987). Atlas No. 3: summary of operations. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-68.

Uye, Shin-ichi.
1985. Resting egg production as a life history strategy of marine planktonic copepods. Bull. Mar. Sci. 37(2): 440–449.

Estimating the annual proportion of nonspawning adults in New Zealand hoki, *Macruronus novaezelandiae*

Mary E. Livingston
Marianne Vignaux
Kathy A. Schofield

National Institute of Water and Atmospheric Research
P.O.Box 14-901 Kilbirnie, Wellington, New Zealand
E-mail address: m.livingston@niwa.cri.nz

Abstract.–Trawl surveys of hoki, *Macruronus novaezelandiae* (Hector) in the Southland and subantarctic areas (Southern Plateau) of New Zealand's Exclusive Economic Zone were carried out in May 1992 and 1993. The proportion of females of each age that would spawn in the coming spawning season (July–August) was estimated on the basis of histological analysis of gonad samples and ageing data. Comparisons were made between numbers of fish at age in these surveys and numbers of fish at age in surveys in November–December 1991 and 1992 to estimate migration before May.

The results indicate that 66% (standard error [SE] of 3%) of females age 7 and over that were on the Southern Plateau in May 1992 would spawn in winter 1992, compared with 65% (SE 2%) in 1993. If the number of hoki estimated to have already migrated out of the survey area in May are included as prespawners, then up to 67% (SE 5%) of adult females were predicted to spawn in winter 1992 and 82% (SE 3%) in winter 1993.

This study confirms that the proportion of adult hoki that spawn in a given year is substantially less than 1. It is not known how much this varies, whether it is with or without trend, or whether it is correlated with any environmental variables. Fishery indicators such as stock and fishery risk are particularly sensitive to the annual proportion of adult hoki that spawn, and it is possible that its variation could obscure any underlying stock-recruitment relationship.

Manuscript accepted 4 September 1996.
Fishery Bulletin 95:99–113 (1997).

Hoki (*Macruronus novaezelandiae* Hector) form New Zealand's largest commercial fishery with an annual catch of about 200,000 metric tons (t). The fish are widely distributed throughout New Zealand's 200-mile Exclusive Economic Zone in depths of 50–800 m, but most commercial fishing is at depths of 200–800 m around the South Island (Fig. 1). Fishing effort is greatest during the July–August spawning season off the west coast and in Cook Strait but also occurs on the Chatham Rise and management areas south of Puysegur Point (hereafter referred to as the Southern Plateau) (Fig. 1) throughout the rest of the year.

Although managed as a single stock, hoki are assessed annually as two stocks (Sullivan and Cordue[1]; Sullivan et al.[2]). There is no genetic evidence for a split, but because morphometric and growth rate differences have been found between the two spawning grounds (Horn and Sullivan, 1996; Livingston and Schofield, 1996), a cautious approach in determining yield has been taken. Hoki are assessed as two stocks by using stock reduction models (Sullivan et al.[2]). Abundance indices estimated from acoustic surveys, trawl surveys, and catch-per-unit-of-effort data on the spawning grounds have been the main inputs to the models (Sullivan et al.[2]).

Of the two stocks, the western stock, which resides primarily on the Southern Plateau and spawns off the west coast of the South Island, is substantially larger than the eastern stock, which resides primarily on the Chatham Rise and spawns in Cook Strait. Juvenile hoki (2–5 yr) of both stocks appear to reside and mix together on the Chatham Rise in relatively shallow water. As the fish reach maturity, it is assumed that they recruit to their respective stocks.

Winter surveys of the Southern Plateau and Chatham Rise have shown that significant numbers of mature-size hoki, both males and females, do not partake in the spawning migration in a given year (Livingston et al., 1991; Hurst and Schofield, 1995).

From trawl surveys of the Southern Plateau in July–August and November–December 1990, it was estimated that the ratio of recruited

[1] Sullivan, K. J., and P. L. Cordue. 1992. Stock assessment of hoki 1992. New Zealand Fisheries Assessment Res. Document 92/12, NIWA Greta Point library, Wellington, New Zealand, 43 p.

[2] Sullivan, K. J., P. L. Cordue, and S. L. Ballara. 1995. A review of the 1992-93 hoki fishery and assessment of hoki stocks for 1994. New Zealand Fisheries Assessment Research Document 95/5, NIWA Greta Point library, Wellington, New Zealand, 45 p.

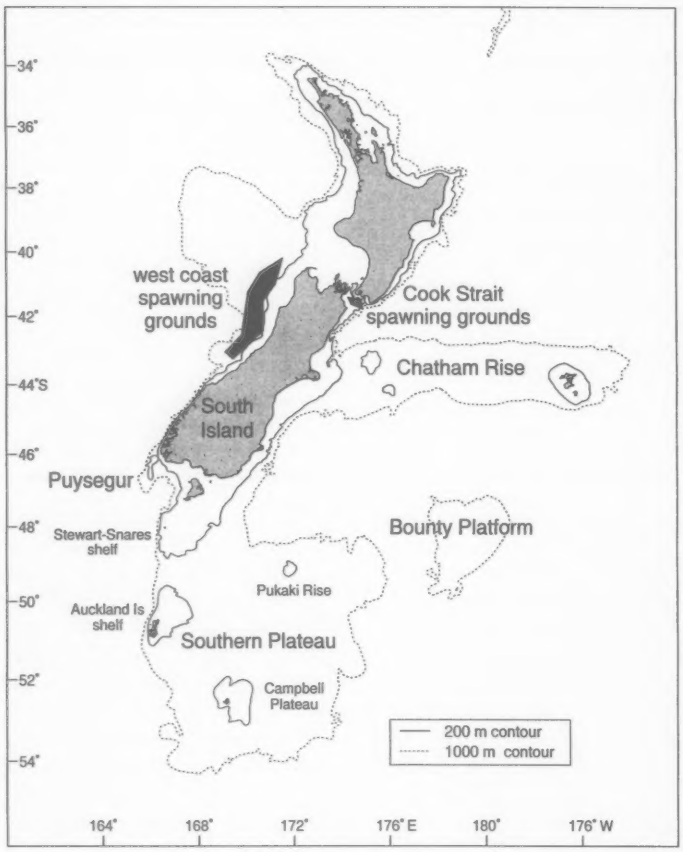


Figure 1

Map of New Zealand showing spawning and feeding grounds of hoki, *Macruronus novaezelandiae*.

biomass of western stock hoki present in winter to the recruited biomass of western stock hoki present in summer was 1:2.05 (Hurst and Schofield, 1995). Hurst and Schofield concluded that the total proportion of adult hoki that spawned in 1990 was between 60% and 75%.

The annual proportion of adult hoki that spawn was incorporated into the stock reduction analysis of hoki as a model parameter for the first time in 1992 (Sullivan and Cordue, 1992). A sensitivity analysis of the response of fishery indicators, such as stock and fishery risk to changes in various model parameters, found that they were particularly sensitive to the proportion of hoki that spawn in a given year (Sullivan and Cordue[1]). In view of this sensitivity, a research program, to estimate more accurately the annual proportion of hoki that spawn and the maturity ogive of hoki at age in the western stock, was initiated.

The spawning season for hoki begins in late June and can extend into mid-September (Sullivan et al.[2]). Large fish tend to spawn earlier than smaller fish, and on the west coast, spawning extends northwards as the season progresses (Langley, 1993). Hoki are not caught in quantity in the vicinity of the west coast outside the spawning season, and there is some evidence from commercial data and trawl survey data to suggest that hoki migrate to the west coast from the Southern Plateau during May–June (Ballara[3]). Female hoki gain up to 40% of their total body weight as their ovaries ripen (Kuo and Tanaka, 1984), but for the remainder of the year, the ovaries are small, weighing less than 1% of total body weight. Ovaries begin to ripen in April before female hoki migrate to their spawning grounds (van den Broek et al., 1981; Kuo and Tanaka, 1984).

Evidence of spawning at other times of the year has not been reported (Kuo and Tanaka, 1984). Preliminary histological work on hoki females collected throughout the spawning season indicates that hoki are either synchronous or group synchronous spawners. That is, their ovaries develop a single set of oocytes in a given season, and these ooocytes are released in a single event (synchronous) or over several spawning events (group synchronous) (West, 1990). The same species in Tasmania develops a single set of oocytes in each season (Gunn et al., 1989). It is unknown whether the proportion of hoki that spawn in a given year is determined by environmental conditions or whether it relates to a shallow recruitment curve or even some nonannual endogenous rhythm.

Our hypothesis was that if hoki develop their oocytes synchronously within each ovary, it should be possible to distinguish developing prespawners from nonspawners prior to the onset of the spawning season and thereby estimate both the proportion of fish that would spawn and a maturity ogive based on histological characterization.

In this study we collected monthly samples to monitor seasonal changes in the ovarian development of hoki prior to spawning. We also used random trawl surveys of the Southern Plateau in December and May in two consecutive years to determine 1) the

[3] Ballara. S. 1995. Natl. Inst. Water and Atmospheric Res., P.O. Box 14-901 Kilbirnie, Wellington, New Zealand. Personal commun.

proportion of female hoki on the Southern Plateau in May that would spawn in the coming season and 2) the proportion of females that already have begun their spawning migration by May. In this paper, we detail 1) the histological basis for classifying hoki as either nonspawners or prespawners and 2) the analyses used to estimate the maturity ogive and the total proportion of fish that would spawn in July or August.

Materials and methods

Trawl surveys

Two sets of surveys were completed: 1) 12 November–23 December 1991 and 17 April–21 May 1992; 2) 14 November–22 December 1992 and 1 May–4 June 1993. The survey area (275,356 km^2) incorporated depths of 300–800 m south of Puysegur Point, excluding rough ground and the Bounty Platform (Fig. 1). The surveys used a two-phase random stratification design (Francis, 1984), and because hoki tend to be near the seabed during daylight, coming up off the bottom to feed at night (Kerstan and Sarhrage, 1980), trawling was carried out during daylight hours only. Trawling procedure and standardization of gear, station, and stratum details are reported for each survey individually by Chatterton and Hanchet (1994), Schofield and Livingston (1994, a and b), and Ingerson et al. (1995).

Length-frequency samples of about 200 female hoki were collected from each tow on a random basis. The length-frequency distribution and the total numbers of fish were scaled up to the total stratum area by using the Trawlsurvey Analysis Program, as described by Vignaux.[4] The scaling was done by assuming a catchability and vulnerability of 1.0 in all surveys. Because these assumptions were unlikely to be valid, the numbers of fish were used only in a relative sense.

Additional samples of 20 female hoki were collected from each tow to measure gonad and total body weight, to identify macroscopic gonad stage, and to obtain histological samples from ovaries. Otoliths were also collected from these fish for ageing. Maturing hoki in the later stages of vitellogenesis can be macroscopically distinguished from resting hoki. The ovaries at that point are swollen, and the individual oocytes, visible to the naked eye, are opaque and creamy pink. Resting and immature ovaries are small and translucent and no oocytes are visible. Previous surveys of hoki in April–May (e.g. van den Broek et al., 1981) reported few hoki that were sufficiently developed to be identified macroscopically as maturing. We therefore obtained histological samples of ovaries as well as recorded their macroscopic appearance. The central portion of the ovary from each sample was preserved at sea in 8%–10% buffered formalin. Samples were later processed to produce thin sections that were stained with standard haemotoxylin and eosin preparations.

Histological staging

In developing a method to distinguish prespawning hoki from nonspawning hoki, we classified ovaries into the stages given by West (1990). Ovaries were classified according to the most advanced oocyte present in the ovary. A summary of these stages (as given by West) is as follows:

Chromatin nucleolar stage	The oocyte is surrounded by a few follicle cells and contains a large nucleus surrounded by a thin layer of cytoplasm. The nucleus has one large nucleolus and several small nucleoli.
Perinucleolar stage	The nucleus has multiple nucleoli at its periphery. Late perinucleolar oocytes may have vacuoles in the cytoplasm.
Yolk vesicle (cortical alveoli) stage	This stage is characterised by the appearance of large numbers of yolk vesicles in the cytoplasm. They increase in size and number to form several peripheral rows. The chorion is visible at this stage.
Vitellogenic (yolk) stage	Small yolk granules which gradually enlarge until they form fluid-filled spheres are typical. The spheres may eventually fuse to form a continuous mass of fluid yolk.
Ripe (mature) stage	The nucleus may be peripheral or may have disintegrated completely.

Criteria to distinguish prespawners from nonspawners were developed from a subsample of ovary sections from each survey and from some commer-

[4] Vignaux, M. 1994. Documentation of trawlsurvey analysis program. NIWA Greta Point Internal Report 225, NIWA Greta Point library, Wellington, New Zealand, 44 p.

cial samples collected from January through August (see below). These criteria (described in the Results section) were then used by an independent reader to classify May 1992 and May 1993 female hoki as prespawners or nonspawners.

Monthly samples were also collected from commercial vessels to monitor hoki development between January and September. Up to 40 ovary samples from a range of adult-size fish were preserved in 8% buffered formalin at the time of capture. Samples were processed in the laboratory, sectioned, and stained with standard haemotoxylin and eosin preparations. Samples were collected mostly from Chatham Rise (Jan–May) and the west coast of the South Island (Jun–Jul) because these were the areas where commercial vessels were operating at that time.

Each fish was staged histologically (as described above) to determine the earliest month in which development began. Five of the most developed fish from each month were then selected for oocyte measurement to confirm that New Zealand hoki are synchronous or group synchronous like their Australian counterparts (Gunn et al., 1989). The mean diameter of 200 oocytes was measured (after Foucher and Beamish, 1980) from each of the five fish.

Ageing

It is unknown whether recruitment to the spawning fisheries is length-driven or age-driven. Observers from the west coast hoki fishery have found spawning hoki as young as 2 years and as small as 42 cm total length, in some years (Sullivan et al.[2]). Because the model used for stock assessment is an age-structured one (Sullivan et al.[2]), fish were aged as part of this study, and all analyses were carried out by using age data. It was also important to age fish so that comparisons of the numbers of fish in each cohort in December and May could be made.

Otoliths from each fish in the histological samples from the May surveys and from the biological samples in December were aged by using the validated ageing method described by Horn and Sullivan (1996). These data were also used to develop age-length keys. Where there were no fish in the sample of a given length, the age-length key was interpolated with nearby values of age.

Proportion of each age class developing to spawn

The proportion of fish in each age class that were classifed as prespawners was estimated for each age stratum from the aged histological samples. The number of fish at each age in each stratum was estimated from the age-length key and the length-frequency distribution in the stratum. For each age class the total number of prespawners was therefore estimated from the proportion of fish that were developing to spawn and from the total number of fish in each stratum. The standard error of these estimates was estimated by using a resampling technique, whereby in each stratum, a sample, the same size as the original sample, was selected (with replacement) from the original sample. The age-length key and proportion of prespawners were calculated from the combined sample of the 15 strata. This process was repeated 1,000 times. The standard error of the estimates was estimated from the standard deviation of the values in 1,000 replicates.

Proportion of adult spawning fish

An estimate $\hat{p}_+$ of the proportion of prespawners in the plus group of adult fish (p_+) can be obtained by using the method described above but by considering all adult fish as a single plus group. However, if some fish had already left the Southern Plateau to spawn before the survey in May, they also should be counted as prespawning fish. This means that the proportion of adult prespawners present on the Southern Plateau in May (p_+) is an underestimate of the total proportion of fish that will spawn (p) as

$$p_+ = \frac{s}{s+ns} \leq \frac{s+g}{s+ns+g} = p, \quad (1)$$

where s is the number of prespawners on the Southern Plateau in May, ns is the number of nonspawners on the Southern Plateau in May, and g is the number of fish that had left the Southern Plateau before May, presumably to spawn.

If we define a migration ratio,

$$x = \frac{g}{s+ns}, \quad (2)$$

to be the ratio of the number of fish which have gone to spawn to the number of fish (both prespawners and nonspawners) that are still in the survey area when the second survey is done, then

$$p = \frac{s+g}{s+ns+g} = \frac{p_+ + x}{1+x}. \quad (3)$$

Thus p equals p_+ when x is zero and increases towards an asymptote of 1 when x is very large.

The migration ratio, x, cannot be estimated very precisely because both trawl surveys will be subject to measurement error and because an unknown number of fish will have died naturally or have been caught between December and May. But to obtain the best estimate of x, the numbers of adult fish on the Southern Plateau in December and May were estimated from the total numbers of fish in the surveys and the proportion that were in the adult age group. The age distributions were estimated from the length-frequency distributions and the age-length keys were calculated from the samples collected for age determination.

In determining the number of fish that moved out of the survey area before May, it is necessary to account for fish that died between December and May. Five months of natural mortality was applied to the number of fish observed in the December surveys to estimate the number of fish that would be expected in the May surveys. The catch taken on the Southern Plateau between December and May in these two years was 10,595 t in 1992 and 8,339 t in 1993. Because the estimated size of the stock was 860,000 t in May 1992 and 1.3 million t in May 1993 (Cordue[5]), fishing mortality was considered to be negligible.

The discrepancy between the number of fish expected in the May survey and the number observed was the maximum number of fish that could be considered to have left the Southern Plateau to spawn. This number was used in Equation 2 to obtain an estimate $\hat{x}$ of the migration ratio x. An estimate of the total proportion of fish that will spawn (p) was calculated by using $\hat{x}$ and an estimate of $\hat{p}_+$ of p_+ in Equation 3. Standard errors of these numbers were calculated by a resampling procedure that included uncertainty regarding the total number of fish in the December and May surveys.

Procedure for estimating the total proportion of adult fish spawning

The estimation procedure for the proportion of adult spawning fish was as follows:

1 The total number of fish on the Southern Plateau in December, N_1 was selected from a normal distribution with mean equal to the estimated value for this survey and with standard deviation equal to the standard error of this estimate. This number of fish was then distributed over the length-frequency distribution (assumed to be known exactly).

2 An age-length key (including ageing error) was generated by sampling with replacement from the fish in the age-length sample from the December survey and was applied to the December length-frequency distribution to estimate the number of adult fish in December, n_1. The number of adult fish expected to be alive in May was calculated by applying the natural mortality M to n_1, as $n_1 e^{-M5/12}$.

3 The same procedures described in 1 and 2 above were applied to the May surveys to obtain the total number of fish on the Southern Plateau in May (N_2) and the number of adult fish in May (n_2)

4 The number of fish apparently missing (n_m) was estimated as

$$n_m = n_1 e^{-M5/12} - n_2 .$$

5 Taken as a fraction of the number n_2 on the Southern Plateau in May, x (the migration ratio) was estimated by

$$\hat{x} = \frac{n_m}{n_2} .$$

6 $\hat{p}_+$ was calculated by using the simulated age-length key and the histological sample as described above. Hence $\hat{p}$ was estimated as

$$\hat{p} = \frac{\hat{p}_+ + \hat{x}}{1 + \hat{x}} .$$

This process was repeated 1,000 times. The standard errors of each of the values was calculated from the standard deviation of the distribution of the 1,000 values.

Results

Trawl surveys

The four surveys were successfully completed with a combined total of 495 stations sampled. Gear parameters were within the range necessary for survey standardization (Hurst et al.[6]), thereby permitting the direct comparison of survey results used for data analysis (Chatterton and Hanchet, 1994; Schofield and Livingston, 1994, a and b; Ingerson et al., 1995).

[5] Cordue, P. 1996. Natl. Inst. Water and Atmospheric Res. P.O. Box 14-901 Kilbirnie, Wellington, New Zealand. Personal commun.

[6] Hurst, R. J., N. Bagley, T. Chatterton, S. Hanchet, K. A. Schofield, and M. Vignaux. 1992. Standardisation of hoki/middle depth time series trawl surveys. NIWA Greta Point Internal Report 194, NIWA Greta Point library, Wellington, New Zealand, 87 p.

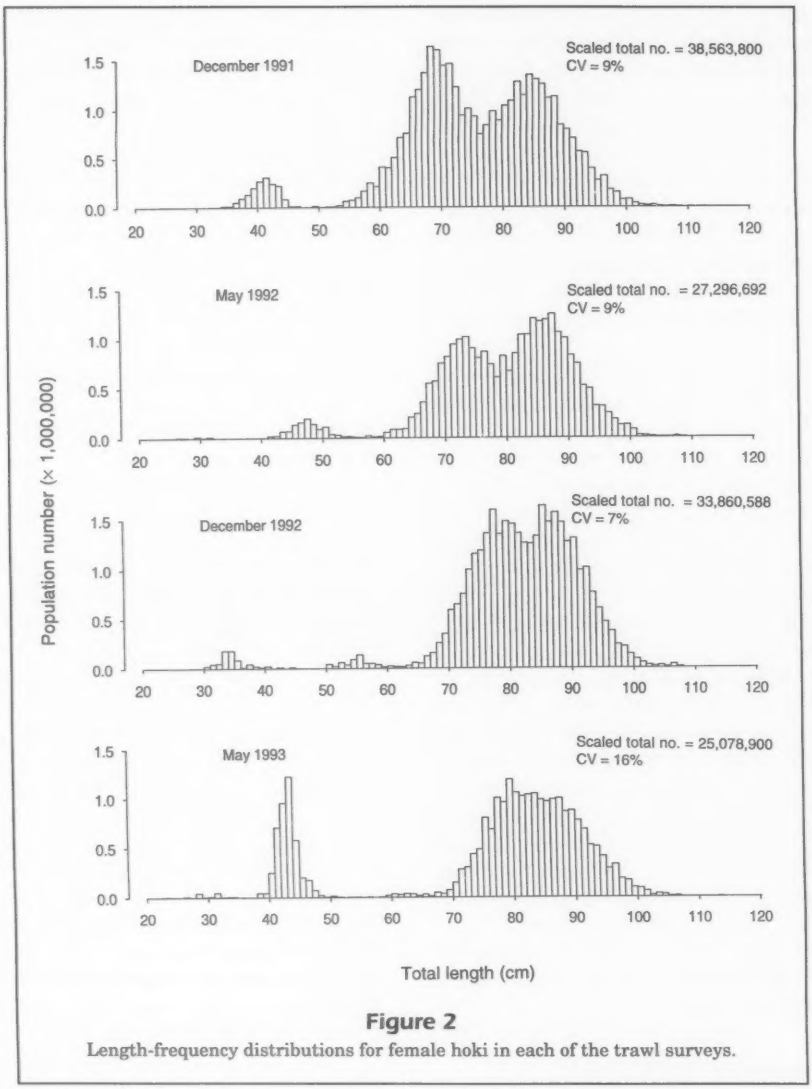


Figure 2

Length-frequency distributions for female hoki in each of the trawl surveys.

The numbers of hoki observed in the May surveys (26.8 million [1992], 24.4 million [1993]) were considerably less than in the December surveys (38.6 million [1991], 34.8 million [1992]) (Fig. 2). In addition, the length-frequency histograms show a decline in bimodality in the adult part of the distribution between May and December (Fig. 2). In December 1991, 56% of females over 50 cm were in strata west of 170°E. In May 1992, 59% were west of this line. In December 1992, 49% were in the west and in May 1993, 68% were in the west.

There were 541 fish in the histological sample in May 1992 and 1,136 fish in the sample in May 1993 (Table 1). In 1992, stratum 1 (300–600 m depth at Puysegur) was not sampled and female fish from every second station in the other strata were sampled. In 1993 female fish from every station in all 15 strata were sampled.

Ageing

There were very few young fish in most strata, and limited numbers of fish in the 1986 cohort, which appeared as age-6 fish in 1992 and as age-7 fish in 1993. Although fish were aged to a maximum age of 19 years, we combined them into a group of age 10^+ and above. The ageing data were also used to develop age-length keys.

Table 1

Percentages of each histological stage observed in female hoki sampled from each survey.

Histological stage	Dec 1991	May 1992	Dec 1992	May 1993
Chromatin nucleolar	0	0	0	0.1
Perinucleolar	100	45.4	100	39.7
Yolk vesicle	0	27.1	0	13.6
Vitellogenic	0	27.5	0	43.3
Ripe	0	0	0	3.3
Number in sample	452	541	1,039	1,136

Histology

Monthly samples of hoki from the Chatham Rise and west coast of the South Island showed little change in oocyte stage in January and February, all being classified as perinucleolar (Table 2). In April, May, and June, larger oocytes of the yolk vesicle and vitellogenic yolk stages were evident. By July and August, females sampled on the west coast of the South Island were vitellogenic or ripe and had hyaline oocytes (Table 2). Oocytes clearly developed as a synchronous group, evidenced by the separation in size of the developing clutch from the reserve fund of chromatin nucleolar and perinucleolar oocytes (Fig. 3).

Table 2

Numbers of hoki monthly samples showing ovarian development on the Chatham Rise and west coast spawning grounds.

Region and month	Histological stage			
	Perinucleolar	Yolk vesicle	Vitellogenic	Ripe
Chatham Rise				
January	22	—	—	—
February	10	—	—	—
March	no sample			
April	6	9	1	—
May	10	9	1	—
West coast				
June	4	3	13	—
July	—	—	10	5
August	—	—	9	5

During the December trawl surveys, most ovaries contained oocytes that could be classified as late perinucleolar (Fig. 4). By May, however, a significant change in oocyte stage had occurred; many ovaries contained cortical alveoli organized into a ring structure and showed increased oocyte size and oil droplets forming around the nucleus (Fig. 5). Because the oocyte stage observed in summer appeared to be a natural holding point in development, we classified a fish with such a stage as perinucleolar. When we saw the same development in fish in the autumn surveys they were classified as nonspawners. Only those fish with a proliferation of cortical alveoli and oil droplets that had begun to form around the nucleus were classified as being at or beyond the yolk vesicle stage and therefore counted as spawners for the coming season.

Table 1 shows the proportion of fish at each stage in each of the surveys. In both December samples, most or all fish were classified as perinucleolar. In contrast, in the May surveys, only 45.4% and 39.7% were in the perinucleolar stages in 1992 and 1993 respectively.

For fish caught during the trawl survey in May 1993, stage of development of the ovary of each fish in the histological sample was also evaluated macroscopically . The number of fish at each histological stage and at each stage of macroscopic gonad development are presented in Table 3. In total, of the 237 ovaries classified as maturing, only two were classified histologically as nonspawners. However, of the 899 ovaries classified as resting, 450 were classified histologically as nonspawners and 449 as prespawners. This finding confirms that physical development for spawning begins before it is apparent macroscopically in the ovaries and reinforces the requirement for histological methods of analysis.

The proportion of prespawners in each stratum was estimated from the aged histological samples from the May surveys (Table 4). If there were not at least two fish in a stratum of a particular age, the proportion was not estimated. Although there were many age-stratum combinations where the proportion of prespawners in a particular age class could not be estimated (mainly for the young fish and for the 1986 cohort), these were not generally found in strata that supported the greatest numbers of hoki of that age class (Table 4).

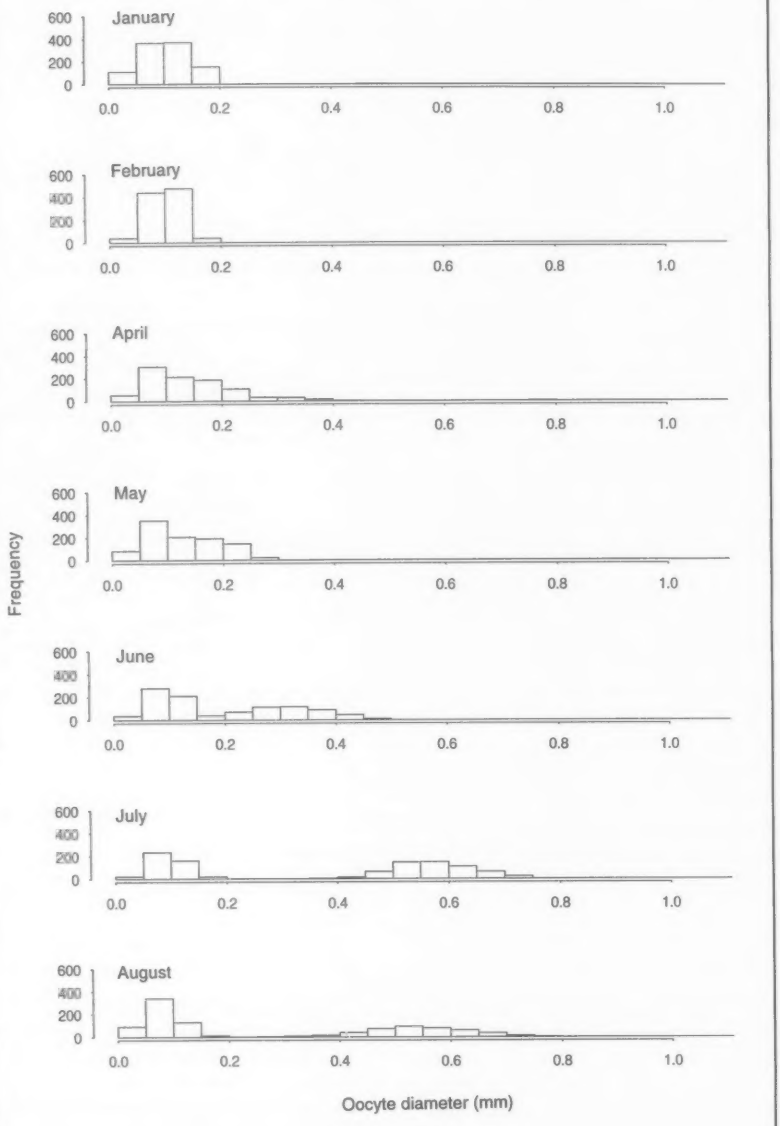


Figure 3

Histograms of oocyte diameter of hoki from samples collected monthly on the Chatham Rise (Jan–Jun 1994) and west coast of the South Island (Jul–Aug 1994) by the commercial fleet.

Proportion of each age class developing to spawn

Table 4 shows the estimated proportion of prespawners in each age class in the 1992 and 1993 May surveys. Table 4 also shows the percentage of fish at each age that were in strata where the proportion of developing fish could be measured (i.e. had at least two fish in the sample). Where this is less than 50%, the estimate is based on fish from only a small fraction of the population, and should not be used. Where it is less than 66%, the estimate might be considered unreliable. In 1992 there were enough data to make a reliable estimate of the proportion of prespawners

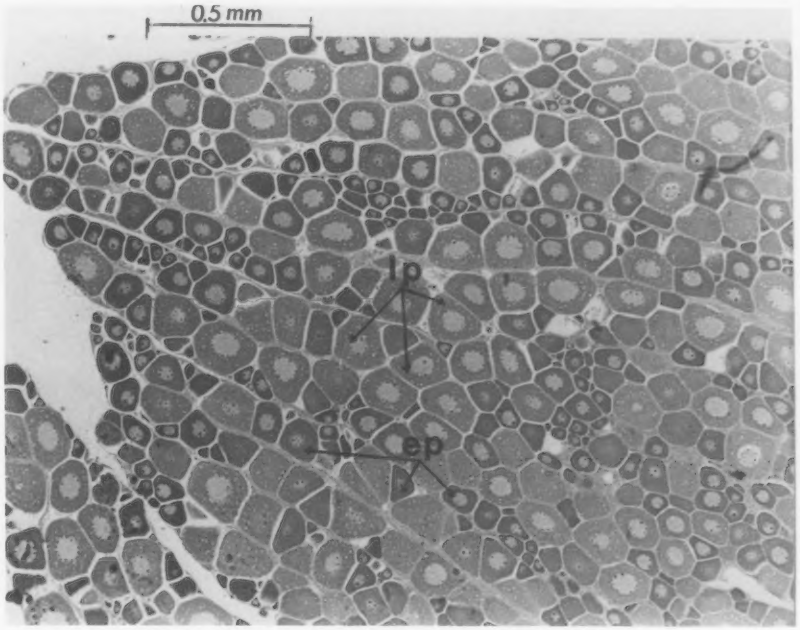


Figure 4

Resting ovary with oocytes in the late perinucleolar stage, December 1991. (ep = early perinucleolar stage oocyte, lp = late perinucleolar stage oocyte (some yolk vesicles present)).

for ages 5, 7, 8, 9, and 10^+, but age 6 (the 1986 cohort) and ages 1, 2, 3, and 4 could not be estimated because the strata with samples contained less than half of the total number of fish in the survey area. In 1993 there were enough data to make a reliable estimate of the proportion of prespawners for ages 5, 6, 8, 9, and 10^+, but ages 3 and 7 (again, the 1986 cohort) were unreliable and ages 1, 2, and 4 could not be estimated.

The estimates of prespawners in each age class for the two surveys are shown in Figure 6. Although there were too few samples to obtain reliable estimates for fish of age 4 and under, it is clear that this proportion would be small. Only 3 of 42 (7%) fish in the sample that were age 4 or younger were classified as prespawners. It is therefore likely that the ogive increases steeply below age 5 before levelling off.

Table 3

Numbers of hoki classified in each histological stage compared with numbers of hoki classifed in each macroscopic stage (May 1993).

	Macroscopic stage		
Histological stage	Resting	Maturing	Total
Nonspawners	450	2	452
Chromatin Nucleolar	1	0	1
Perinucleolar	449	2	451
Prespawners	449	235	684
Yolk Vesicle	154	1	155
Vitellogenic	295	197	492
Ripe	0	37	37
Grand total	899	237	1,136

Proportion of adult fish spawning

Figure 6 suggests that there may have been some increase in the proportion of prespawners up to age 8 in 1992 but that in 1993 the numbers of prespawners did not increase after age 5.

If we assume that any increase after age 7 is not significant, then the asymptotic values of the ogives in Figure 6 represent the measured proportion of adult prespawners (p_+) in the years 1992 and 1993. Following a procedure identical to that above, but considering only fish aged 7 and over, the proportion of adult prespawners in the survey area was estimated as 66% in 1992 (SE 3%) and 65% in 1993 (SE 2%).

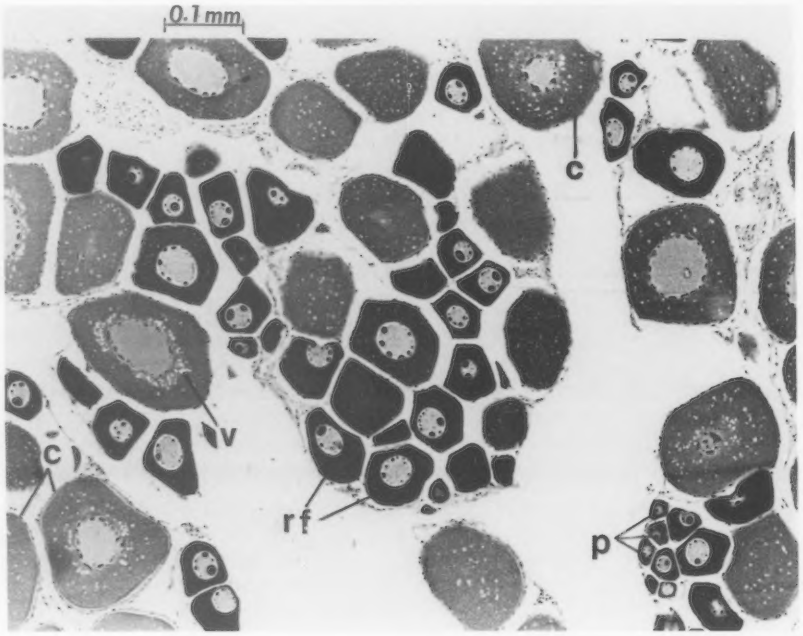


Figure 5

Histological sample from May 1993 showing some oocytes that had developed into the yolk vesicle stage. Note the circumnuclear distribution of the oil droplets that are beginning to form. (c = chorion, p = primary oocytes at chromatin nucleolar stage, rf = nondeveloping reserve fund oocytes at perinucleolar stage, v = vesicle ring around nucleus of yolk vesicle stage oocyte).

Table 4

Estimated total numbers of female fish, numbers of female fish in sampled strata, percentage of female fish in strata covered by sampling, numbers of prespawners, proportion of prespawners with standard error (SE), for each age class in the May surveys (NA indicates that the value could not be estimated). SE = standard error.

	Age class									
	1	2	3	4	5	6	7	8	9	10+
May 1992										
Total in survey (× 1,000)	54	1,182	0	1,648	7,645	557	2,101	6,025	3,407	4,150
In sampled strata	0.00	511	0	691	7,458	130	1,478	5,973	3,387	4,132
% in sampled strata	0	43	NA	42	98	23	70	99	99	100
Prespawners (× 1,000)	0.00	0.00	0.00	132	3,333	35	844	4,065	2,323	2,652
Proportion spawning	NA	0.00	NA	0.19	0.45	0.27	0.57	0.68	0.69	0.64
SE	NA	NA	NA	0.10	0.05	0.26	0.08	0.05	0.05	0.05
May 1993										
Total in survey (× 1,000)	95	3,573	142	135	2,614	6,986	338	1,777	4,340	4,447
In sampled strata	0	0	83	29	2,586	6,986	183	1,739	4,304	4,418
% in sampled strata	0	0	59	21	99	100	54	98	99	99
Prespawners (× 1,000)	0	0	0	0	1,649	3,928	123	1,143	2,967	2,782
Proportion spawning	NA	NA	0	0	0.64	0.56	0.67	0.66	0.69	0.63
SE	NA	NA	NA	NA	0.05	0.03	0.18	0.06	0.03	0.03

Table 5

Estimation of total proportion spawning (p) of age-7+ hoki based on (p_+) the proportion of prespawners on the Southern Plateau and on the number of hoki in the plus group on the Southern Plateau in December 1991, 1992, and May 1992, 1993. (n = number of hoki × 10^3, SE = standard error; M = natural mortality).

Year	$M = 0$ n (SE)	$M = 0.25$ n (SE)	$M = 0.3$ n (SE)
1992			
Observed, December 1991	17, 945 (1,700)	17, 945 (1,700)	17, 945 (1,700)
Observed, May 1992	15, 682 (1,400)	15, 682 (1,400)	15, 682 (1,400)
Expected, May 1992	17, 945 (1,700)	16, 170 (1,500)	15, 837 (1,500)
Missing, May 1992	2, 263 (2,200)	488 (2,100)	155 (2,100)
Migration ratio	0.14 (0.16)	0.03 (0.14)	0.01 (0.14)
Proportion spawning	0.70 (0.05)	0.67 (0.05)	0.66 (0.05)
1993			
Observed, December 1992	23, 250 (1,800)	23, 250 (1,800)	23, 250 (1,800)
Observed, May 1993	10, 902 (1,700)	10, 902 (1,700)	10, 902 (1,700)
Expected, May 1993	23, 250 (1,800)	20, 950 (1,600)	20, 518 (1,600)
Missing, May 1993	12, 348 (2,400)	10, 048 (2,300)	9, 616 (2,300)
Migration ratio	1.13 (0.43)	0.92 (0.39)	0.88 (0.38)
Proportion spawning	0.84 (0.03)	0.82 (0.03)	0.81 (0.04)

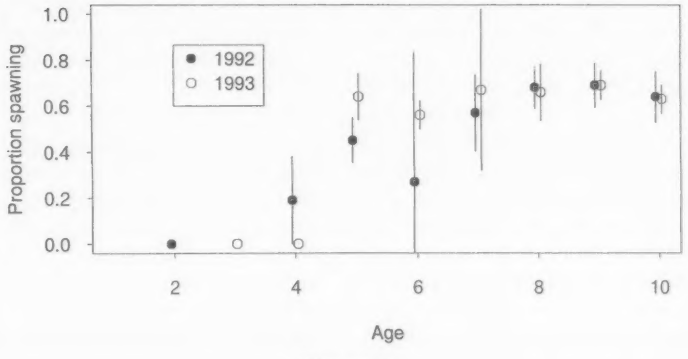


Figure 6

Proportion of prespawners at age from 1992 and 1993 surveys. The error bars indicate two standard errors.

Table 5 shows the estimates of the total proportion of adult fish that will spawn (i.e. including those fish that have already left the area) calculated as above. The calculations were done with three estimates of natural mortality M, including the best estimate $M = 0.25$, and two bounding values $M = 0$ and $M = 0.3$ (Sullivan et al.[2]). Table 5 shows that this makes little difference to the estimate of $\hat{p}$. Standard errors of the estimates were calculated by using the resampling technique.

The best estimate of the total proportion of adult fish that would have spawned in the 1992 winter season was 0.67 (SE 0.05, with $M = 0.25$). If M is as high as 0.3 or as low as 0, the estimate of p decreases to 0.66 or increases to 0.70 respectively. The best estimate of the total proportion of adult fish that will spawn in the 1993 winter season was 0.82 (SE 0.03). If M is as high as 0.3 or as low as 0, the estimate of p is 0.81 or 0.84 respectively.

Figure 7 shows the effect of the estimate of $\hat{x}$ on the estimate of $\hat{p}$ for 1992 and 1993. In each plot there are three curves for $\hat{p}$ as a function of $\hat{x}$. The solid curve is the function given the estimated value of $\hat{p}_+$ (0.66 in 1992 and 0.65 in 1993). The two dot-

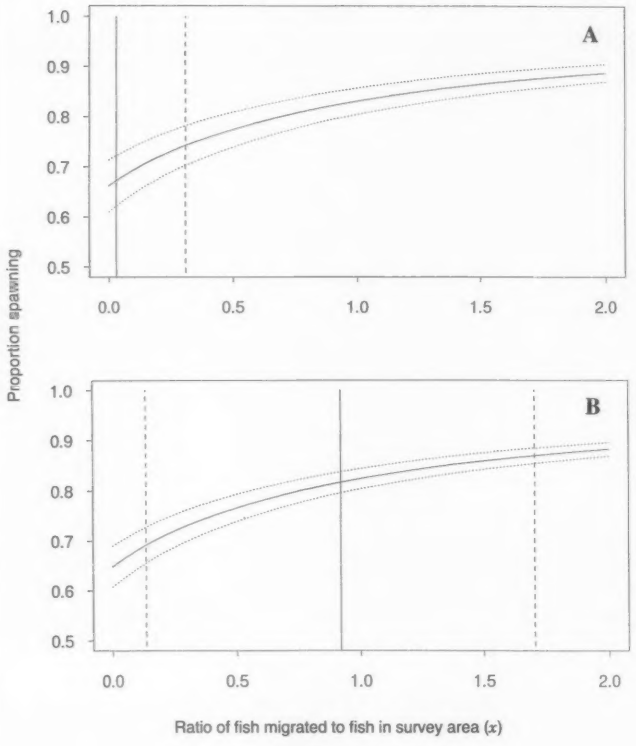


Figure 7

Estimated total proportion spawning (p) among age-7+ fish as a function of the migration ratio (x) in (**A**) 1992 and (**B**) 1993.

ted curves are the functions at plus and minus two standard errors of this value.

The solid vertical lines show the value of $\hat{x}$ with $M = 0.25$. The two dashed vertical lines shown are at plus or minus two standard errors of this value. Clearly the value of $\hat{x}$ is not at all well known. However, the function is changing slowly over this range; therefore it is still possible to obtain a useful estimate of p.

Discussion

The number of studies that have attempted to measure the level of nonspawning in adult fish and to determine its effect on population estimates used for stock assessment appears to be few. It is often assumed that although the steepness of the maturity ogive varies among species, it will always level out at or near 100% spawning (e.g. Hislop, 1984). Species documented to reach less than 100% spawning include orange roughy, *Hoplostethus atlanticus*, off southeast Australia at 55% (Bell et al., 1992), the brackish water burbot *Lota lota* (L) in the Baltic sea at 70% (Pulliainen and Korhonen, 1990), and the estuarine yellow-fin (surf) bream, *Acanthopagrus australis* at 50% (Pollock, 1984). Although the annual proportion of hoki that spawn is similar to that of these other species, the other studies did not adjust for population size or take migratory movements into account. Our estimates for hoki are close to the range indicated by Hurst and Schofield (1995) who did adjust for population size.

There were some potential sources of error that we could not measure. First, the number of undeveloped fish surveyed on the Southern Plateau in May that were classified as nonspawners, which could have developed late and gone on to spawn, is unknown. This would lead to an underestimate of the proportion of prespawners. Second, if a number of fish remained undeveloped but migrated to the spawning ground anyway, the number of fish that

would leave the Southern Plateau after May would be underestimated. Third, the number of developing fish in May that could have resorbed their eggs and not gone on to spawn after all could lead to an overestimation of the total proportion spawning. Other sources of error concern changes in catchability and vulnerability between surveys and the difficulty of detecting any bias or size selectivity when sampling a population with the trawl.

With regard to the first source of error above, it was encouraging that hoki collected in April showed significant signs of development compared with those collected in February (Table 2). The most likely fish to be affected by late development are the younger, smaller fish because they spawn later in the season compared with the older, larger fish which spawn at the beginning of the season (Langley, 1993). Because we estimated the proportion of hoki age 7 years and above that were spawning, the problem was minimized.

With regard to the second source of potential error, undeveloped hoki of age 4 and greater are not caught on the spawning grounds during the spawning season (Langley, 1993), suggesting that there may be 100% spawning among hoki that migrate to the west coast spawning grounds. We have no data on the number of fish that could resorb their eggs before the spawning season, but none were found in the May samples in this study.

With regard to the trawl survey technique, it is possible that there are systematic changes in catchability or vulnerability between December and May. We considered it more likely, however, that the changes in fish numbers were real, and that some fish had already migrated away from the Southern Plateau before the May survey, particularly in 1993 when the survey took place later than in 1992.

The ratio of the number of missing fish to the number of fish present on the Southern Plateau (the migration ratio, x) can also be expressed in terms of the proportion of fish that have already migrated (p_m)

$$x = \frac{p_m}{1 - p_m}$$

or, equivalently

$$p_m = \frac{x}{1 + x}.$$

Both x and p_m change as fish leave the Southern Plateau. In December, when no fish have migrated, both $x = 0$ and $p_m = 0$. If a survey were to be done at a point when 33% of the fish had migrated, or $p_m = 0.33$, there would be one fish missing for every two fish still in the survey area, and x would be 0.5. By July 1993, when an estimated 82% of fish have gone to spawn, $\hat{p}_m$ is 0.82 and $\hat{x}$ has increased to 4.6. Therefore, in May 1993, when $\hat{x} = 0.92$ and $\hat{p}_m = 0.48$, we can estimate that more than half (58.5%) of the fish that were going to spawn had already gone.

This is, of course, poorly estimated, as is x, but it is higher than was expected before the surveys were done. If the survey results are correct, they suggest that in May 1993, fish had already started to migrate in large numbers. The survey in May 1993 began two weeks later in the year than that in 1992, indicating that May is a critical time for the spawning migration of hoki. This interpretation is supported by the change in distribution of fish from the east to the west between December and May in 1993, but not in May 1992. If, however, our estimates of the numbers of fish that have migrated away from the Southern Plateau by May are incorrect (e.g. because of changes in catchability or vertical availability between December and May, or because not all fish have begun to develop by May), then the proportion of prespawners on the Southern Plateau in May could be used as a lower limit of the proportion spawning of the total population. Given that a standardized trawl survey technique was the best method available to us to sample the adult hoki population, we believe that it would be difficult to improve on the estimates of proportion spawning obtained.

The 4–6 yr age classes show different proportions of prespawners in each year, with more 4 year olds but with fewer 5 and 6 year olds developing to spawn in 1992 than those in 1993 (Fig. 6). Differences in the proportion of spawning fish in the younger age classes could also relate to the preceding spawning history of a particular age class.

Although every year many hoki spawn on the west coast of the South Island, it is clear that a large number of individuals do not. Species that exhibit such behavior usually have a major accessory activity that requires a significant amount of energy in addition to spawning itself (Bull and Shine, 1979). Hoki migrate over vast distances of about 1,500 km from the Southern Plateau to the west coast spawning grounds. The energy cost incurred during migration may be so high that there is not enough left for egg production the following year.

Lack of food and migration distance have been suggested as reasons for lack of spawning among orange roughy (Bell et al., 1992) and yellow fin bream (Pollock, 1984). However, Pulliainen and Korhonen (1990) found that nonspawning burbot maintained a condition similar to that of spawning burbot and ruled out low food supplies as an explanation for nonspawning adults.

Within species where different populations show different levels of nonspawning, it has been found

that the lowest frequencies are usually associated with increased stress, such as poorer quality habitat, food shortage, or a shorter growing season (Bull and Shine, 1979). Nonspawning condition has been induced experimentally for several species by reducing their food supply (e.g. haddock [Hislop et al., 1978]; Newfoundland winter flounder [Burton and Idler, 1987]; and plaice [Horwood et al., 1989]).

Nutrients are in good supply and do not limit primary production on the Campbell Plateau (which forms a major portion of the Southern Plateau survey area); however, chlorophyll concentrations over depths of 450 m or greater are generally low (Heath and Bradford, 1980). Heath and Bradford suggest that because of this and other characteristics of the area, there never will be a well-developed zooplankton community with a high biomass on the Campbell Plateau. Areas of higher productivity are found on the island shelves and shallow rises in the area, or downstream from the Campbell Plateau itself. The energetics of the food chain in the study area are not known. It is possible that the lack of high primary and secondary productivity in the area contributes toward nonreproduction in some hoki from year to year.

Whatever the cause, nonspawning among adult hoki has important implications for stock assessment and risk estimation in the management of New Zealand hoki stocks. The proportion of fish that migrate to spawn is a scaling factor that relates the number of fish observed during the spawning season (using tools such as CPUE and acoustics) to the total population. It also provides a buffer between the total stock and the population vulnerable in any one year to the greatest fishing effort that is applied during the spawning season. Further, it reduces the stock size, which is needed for calculating the stock-recruit relationship used in predicting future recruitment.

The effect of these factors may be minimal if the level of nonspawning fish is constant. If, however, the proportion spawning varies from year to year, as suggested by our study, the implications for modelling may be both complex and important.

It is likely that there are other species not necessarily related to hoki that could also have significant and variable proportions of nonspawning fish. There may therefore be major implications for the stock assessment of those species as well. Any stock assessment tool that is used to obtain an estimate of absolute abundance from a spawning population (e.g. acoustics, egg-production method) should take nonspawning into account. It is also important that the effect of nonspawning on any stock-recruitment relationship (assumed or measured) be taken into account because one of the more serious difficulties in determining the stock-recruitment relationship of any species is obtaining a reliable measure of the spawning stock size (Hilborn and Walters, 1992). Further, the stock-recruitment dynamics of a population could be masked, particularly if the level of nonspawning is correlated to some environmental factor or autocorrelated because of some inherent life strategy, such as improved longevity or increased egg size.

We have shown that nonspawning among adult hoki is substantial, and it has important consequences for stock assessment. For these reasons, it is clear that a better understanding of its variability, and how widespread its occurrence might be among other species, would be useful for fisheries management worldwide.

Acknowledgments

We thank Peter Horn for ageing the samples; Kevin Sullivan, Patrick Cordue, and Len Tong for useful discussions; the scientific staff who participated in the trawl surveys; the officers and crew of GRV *Tangaroa*; and the scientific observers for collecting samples from commercial vessels. We also thank three anonymous reviewers for their comments and suggestions.

Literature cited

Bell, J. D., J. M. Lyle, C. M. Bulman, K. J. Graham, G. M. Newton, and D. C. Smith.
1992. Spatial variation in reproduction and occurrence of non-reproductive adults in orange roughy, *Hoplostethus atlanticus* Collett (Trachichthyidae), from south-eastern Australia. J. Fish Biol. 40:107–122.

Bull J. J., and R. Shine.
1979. Iteroparous animals that skip opportunities for reproduction. Am. Nat. 114(2):296–316.

Burton, M. P., and D. R. Idler.
1987. An experimental investigation on the non-reproductive, post-mature state in winter flounder. J. Fish Biol. 30:643–650.

Chatterton, T. D., and S. M. Hanchet.
1994. Trawl survey of hoki and associated species in the Southland and Sub-Antarctic areas, November–December 1991 (TAN9105). N.Z. Fish. Data Rep. 41, 55 p.

Foucher, R. P., and R. J. Beamish.
1980. Production of non-viable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37:41–48.

Francis, R. I. C. C.
1984. An adaptive strategy for stratified random trawl surveys. N.Z. J. Mar. Freshwater Res. 18:59–71.

Gunn, J. S., B. D. Bruce, D. M. Furlani, R. E. Thresher, and S. J. M. Blaber.
1989. Timing and location of spawning of blue grenadier *Macruronus novaezelandiae* (Teleosti: Merlucciidae) in Australian coastal waters. Aust. J. Mar. Freshwater Res. 40:97-112.

Heath, R. A., and J. M. Bradford.
1980. Factors affecting phytoplankton production over the Campbell Plateau, New Zealand. J. Plankton Res. 2:169–181.

Hilborn, R., and C. J. Walters.
1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, London, 570 p.

Hislop, J. R. G.
1984. A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway punt in the North sea. *In* G. W. Potts, and R.J. Wootton, (eds.), Fish reproduction strategies and tactics, p. 311–329. Academic Press, London.

Hislop, J. R. G., A. P. Robb, and J. H. Gauld.
1978. Observations on effects of feeding level on growth and reproduction in haddock *Melanogrammus aeglefinus* (L) in captivity. J. Fish Biol. 13:85–98.

Horn, P. L., and K. J. Sullivan.
1996. Validated aging methodology using otoliths, and growth parameters for hoki (*Macruronus novaezelandiae*) in New Zealand waters. N.Z. J. Mar. Freshwater Res. 31:161–174.

Horwood, J. W., M. G. Walker, and P. Witthames.
1989. The effect of feeding levels on the fecundity of plaice (*Pleuronectes platessa*). J. Mar. Biol. Assoc. U.K. 69:81–92.

Hurst, R. J., and K. A. Schofield.
1995. Winter and summer trawl surveys of hoki south of New Zealand, 1990. N. Z. Fish. Tech. Rep. 43, 55 p.

Ingerson, J. K. V., S. M. Hanchet, and T. D. Chatterton.
1995. Trawl survey of hoki and associated species in the Southland and Sub-Antarctic areas, November–December 1992 (TAN9211). N.Z. Fish. Data Rep. 66, 44 p.

Kerstan, M., and D. Sahrhage.
1980. Biological investigations on fish stocks in waters off New Zealand. Mitteilungen Inst. Seefischerei Bundesforschungsanstalt Fischerei 29, Hamburg, 187 p.

Kuo, C. L., and S. Tanaka.
1984. Maturation and spawning of Hoki *Macruronus novaezelandiae* (Hector) in waters around New Zealand. Bull. Jpn. Soc. Sci. Fish. 50:397-402.

Langley, A. D.
1993. Spawning dynamics of hoki in the Hokitika Canyon. N.Z. Fish. Tech. Rep. 34, 29 p.

Livingston, M. E., and K. A. Schofield.
1996. The discrimination of hoki groups (*Macruronus novaezelandiae*) in New Zealand waters using morphometrics. N.Z. J. Mar. Freshwater Res. 31:197–208

Livingston, M. E., Y. Uozumi, and P. H. Berben.
1991. Abundance, distribution and spawning condition of hoki and other mid-slope fishes on the Chatham Rise July 1986. N.Z. Fish. Tech. Rep. 25, 47 p.

Pollock, B. R.
1984. Relations between migration, reproduction and nutrition in yellowfin bream *Acanthopagrus australis*. Mar. Ecol. Prog. Ser. 19:17—23.

Pulliainen, E., and K. Korhonen.
1990. Seasonal changes in condition indices in adult mature and non-maturing burbot *Lota lota* (L.), in the north eastern Bothnian Bay, northern Finland. J. Fish Biol. 36:251–259.

Schofield, K. A., and M. E. Livingston.
1994a Trawl survey of hoki and associated species in the Southland and Sub-Antarctic areas, April–May 1992 (TAN9204). N.Z. Fish. Data Rep. 45, 38 p.

1994b Trawl survey of hoki and associated species in the Southland and Sub-Antarctic areas, May–June 1993 (TAN9304). N.Z. Fish. Data Rep. 47, 39 p.

van den Broek, W. L. F., K. Tokusa, and H. Kono
1981. A survey of demersal fish stocks in waters south of New Zealand, March–May 1982. Fish. Res. Div. Occas. Publ. 44, 51 p.

West, G.
1990. Methods of assessing ovarian development in fishes: a review. Aust. J. Mar. Freshwater Res. 41:199-222.

Structure and dynamics of the fishery harvest in Broward County, Florida, during 1989

James E. McKenna Jr.

Florida Marine Research Institute, Florida Department of Environmental Protection
100 Eighth Ave. S.E., St. Petersburg, FL 33701
Present Address: Tunison Laboratory of Aquatic Science
National Biological Service, 3075 Gracie Road,
Cortland, New York 13045

E-mail address: 76743.1403@compuserve.com

Abstract.—Florida's rich fisheries are among the state's most valuable resources, attracting the interest of fishermen, divers, and others. Commercial and recreational exploitation of these resources has altered the abundances of some valuable species; consequently fishery regulations and a system to monitor landings have evolved in response.

Until now, the biological structure of the multispecies harvest has not been examined. Landings from commercial trips in Broward County during 1989 were used to describe the structure and seasonal dynamics of that harvest. Cluster analysis classified fishing trips into distinct groups associated with different habitats and gear. Swordfish landings dominated this low-diversity harvest. There were significant seasonal changes in the species assemblages landed. However, most species associations were weak and negative.

The observed structure of the Broward County harvest reflects the selectivity inherent in commercial fishing. It is a balance between the differential availability of various species to the gear used and the market values driving the fishermen to select some species and discard others. Seasonal changes in the harvest structure reflect changes in the availability of various species and in the fishermen's ability to adapt to these changes by switching to alternate target species. The strong biases introduced by the selectivity of this system can obscure events in the natural system and provide little insight into the changes in the natural fish community.

Manuscript accepted 4 September 1996.
Fishery Bulletin 95:114–125 (1997).

Florida waters are rich in fish and shellfish. Although the greatest diversity is found in coral reef habitats (Starck, 1968), hundreds of species are found throughout Florida's marine waters (Anderson and Gehringer, 1965; Herrema, 1974; Gilmore, 1977). Statewide, commercial landings are reported to the Department of Environmental Protection by using 531 different species codes, some of which represent groups of species. This assemblage is two to three times larger than any other state's marine fishery resource.

Historically, fish communities containing commercially valuable species have been strongly influenced by human activities, especially fishing (e.g. Cushing, 1961; Idyll, 1973; Beddington and May, 1982; Gulland, 1983; Beddington, 1986; Sissenwine, 1986; Laevastu and Favorite[1]). Florida's fishery resource has been intensely exploited both commercially and recreationally for many years (e.g. Nakamura and Bullis, 1979; Newlin, 1991). Bohnsack et al. (1994) have provided a good description of the complexity of Florida fisheries, explored the effects of exploitation, and discussed the difficulties in interpreting available landings data. The effects of exploiting this multispecies resource have been demonstrated for a few valuable species (Spanish mackerel: Williams et al.[2]; king mackerel: Fable, 1990; spiny lobster: Moe, 1991; red drum: Goodyear[3]; billfishes: Anonymous[4]; swordfish: Anonymous[5]; red grouper: Goodyear and Schirripa[6]). However,

[1] Laevastu, T., and F. Favorite. 1978. The control of pelagic fishery resources in the eastern Bering Sea. Northwest and Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115. Proceedings report. (Manuscript.)

[2] Williams, R. O., M. D. Murphy, and R. G. Muller. 1985. A stock assessment of the Spanish mackerel, *Scomberomorus maculatus*, in Florida. Unpublished, third draft. Prepared for the Florida Marine Fisheries Commission, 2540 Executive Center, Circle West, Tallahassee, FL 32301, 65 p.

[3] Goodyear, C. P. 1987. Status of red drum stocks in the Gulf of Mexico. Contribution report CRD 86/87-34, Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Dr., Miami, FL 33149, 49 p.

[4] Anonymous. 1982. Draft fishery management plan, draft environmental impact statement, and regulatory impact review for the Atlantic billfishes: white marlin, blue marlin, sailfish and spearfish. South Atlantic Fishery Management Council, 1 South Park Circle, Suite 306, Charleston, SC, report G#27 BF Fmwk 8/82, 64 p.

[5] Anonymous. 1991. Reference paper on 1991 swordfish stock assessments by SCRS swordfish assessment group. Miami Laboratory, Southeast Fisheries Science Center, NMFS, NOAA, Miami, FL, rep. SCRS/91/16, 193 p.

[6] Goodyear, C. P., and M. J. Schirripa. 1991. The red grouper fishery of the Gulf of Mexico. Miami Laboratory, Southeast Fisheries Science Center, NMFS, NOAA, 75 Virginia Beach Dr., Miami, FL 33149. Contribution rep. MIA-90/91-86, 79 p.

only anecdotal reports of associations among harvested species exist.

Concern about the effects of harvesting this resource has stimulated research on the structure and dynamics of Florida's marine fish community. Structure of the harvest is related to the structure of the natural community and to the economics influencing fishermen's behavior. It integrates the differential fishing mortality affecting the natural community. In 1984, the Florida Department of Environmental Protection (FDEP) established a trip-ticket reporting system (Marine Fisheries Information System) to monitor the fishery harvest and provide a database of basic information on commercial landings from this resource. All dealers buying fish from fishermen or fishing for themselves must report the amounts of all species landed on each fishing trip. These records normally represent those species brought to shore on a single fishing trip and sold (landed). They do not include species or individuals caught and subsequently discarded, those used as bait, or those brought to shore but not sold. Harvesting occurs in many different ways (e.g. traps, nets, hook-and-line) and can have a variety of effects on the fishery resource and the natural community as a whole. A better understanding of the multispecies resource and the potential effects of the harvest can be gained by relating the structure and its variability to what is known about the natural fish assemblage and the harvesting behavior of fishermen. This study uses commercial landings data collected by the Marine Fisheries Information System (MFIS) to examine the structure and temporal dynamics of the harvest in Broward County, Florida (Fig. 1), during 1989.

Methods

The MFIS database includes, but is not limited to, information on the weight of each species landed from each commercial fishing trip, the date on which those landings occurred, and the time spent fishing. Information on depth and fishing area were provided on a voluntary basis in 1989 but the spaces for reporting such information were often left blank by reporting dealers. Information on gear used was not provided.

All commercial landings reported from Broward County during 1989 were used in this analysis. This subset of the MFIS database was chosen for this study because Broward County fisheries landings are some of the most valuable in the state. Furthermore, because 3,246 landings records (out of more than 2.5 million) exist, it is computationally one of the most manageable data sets available. Each month of data was analyzed separately in an attempt to detect seasonal trends in species assemblage structure. Monthly assemblages were constructed on the basis of total monthly landings of each species.

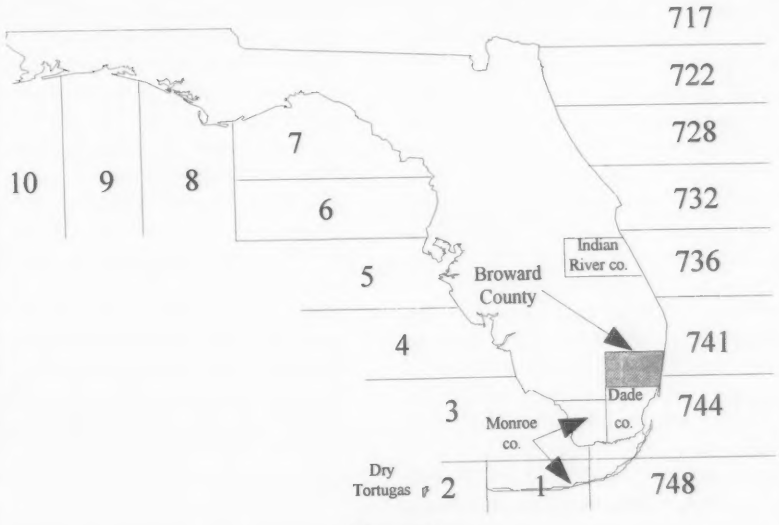


Figure 1

Designations of fishing areas used by the Florida Marine Information System. Broward County's location on the southeast coast is indicated by the shaded area.

Diversity was described by using the Shannon-Wiener Information Index (H') (Shannon and Weaver, 1949) and its component parts, richness (number of species) and evenness (V') (Pielou, 1977).

$$H' = -\sum p_i \log_e p_i$$

$$V' = H'/\log_e s^*,$$

where p_i is the proportion of species i and s^* is the number of species in the entire community (Pielou, 1977). In this study, the value of s^* was set to the total number of species landed in a given month when calculating evenness per ticket, and to the total number of species (76) landed over the entire year when calculating evenness per month.

Heterogeneity ratios (HR) (HR actually measures beta diversity, which is an index of dissimilarity, Kobayashi, 1987) were calculated to measure the similarity between all pair-wise comparisons of monthly assemblages. All pair-wise combinations of assemblages were tested for significant differences (α=0.05) by using a Monte Carlo simulation technique that compares the observed number of species common to the two assemblages of interest with that expected from randomly extracting two assemblages (each having the same number of species as one of the observed assemblages) from the community as a whole (FAUNSIM) (Raup and Crick, 1979; McKenna and Saila, 1991).

A nonhierarchical cluster analysis (SAS FASTCLUS, SAS, 1985) was applied to classify the trips according to the species assemblage landed each month. A maximum of 3 iterations and 20 clusters were specified. No minimum radius was specified. The REPLACE = option was set to RANDOM so that a simple pseudorandom sample of observations was chosen as initial cluster seeds. The DRIFT option was specified to adjust cluster seeds to their cluster mean each time an observation was added.

Spearman's rank correlation analysis was performed on every pair-wise combination of monthly species landings, on a trip-by-trip basis, to test for significant associations. A Z-test was applied to determine the significance of each correlation at the 0.01 level (Freund, 1970, p. 311–313).

Results

A total of 1,355,421 kg (2,981,926 pounds) of finfish and shellfish were landed in Broward County during 1989 according to the 3,246 commercial fishing trips reported (Table 1). The monthly average was 112,840 kg (248,247 pounds) ranging from 41,889 kg (92,156 pounds) to 178,489 kg (392,675 pounds) (Fig. 2).

Geography of the harvest

Florida's commercial fishing fleet is, in general, artisanal (small boats operating near shore). In 1989, 907 saltwater products licenses, 61 wholesale dealer licenses, and 408 retail dealer licenses were issued to residents of Broward County. Most fishermen worked in the waters immediately adjacent to the Broward County coast. The fishing area (Fig. 1) was reported for 76% of the trips landing fish in Broward County. According to those trip-tickets that included fishing area, fishermen harvested from areas 741 (45%) or 744 (37%) on 82% of fishing trips. The number of trips diminished as one moved away from the Broward County coast. Fish were caught from areas as far north as the waters off Indian River County (area 736), as far south and west as the Tortugas (area 2). Rarely, landings were reported from waters of Florida Bay off mainland Monroe County (area 3).

Diversity

Diversity of landed species was low in comparison with the natural diversity of this subtropical community. A total of 76 species (or groups of species) were landed in Broward County in 1989. Diversity (H') of the total harvest was 1.86; evenness (V') was 0.43. Mean monthly diversity (1.88) was almost identical to that for the total harvest (Table 2). Monthly evenness values varied between 0.31 and 0.62, a mean of 0.43. Diversity and evenness followed roughly sinusoidal patterns throughout the year, with peaks in September (H'=2.69, V'=0.62) approximately double the minimum value in May (H'=1.36, V'=0.31). Monthly richness approached 50 species most of the year; June (36) and July (44) had the lowest values, April (54) and November (55) had the highest values. Despite the fact that the waters off Broward County contained a relatively rich (at least 76 species commercially harvested) multispecies fish community, as many as half of all trips in any given month landed only a single species. Mean alpha diversity (defined here as diversity based on landings from a single fishing trip) was low (0.44) and showed little variability (Fig. 3). It was greatest in January and February and dropped to about 60% of those values for the rest of the year. Richness displayed a very small range (2.5–3.5 species per trip).

Similarity

Beta diversity (HR) among pair-wise comparisons of monthly assemblages ranged from 1.05 to 1.26 (Table 3). The species assemblages landed in March and September were most similar and those landed in

Table 1

Fish and shellfish landed in Broward County, Florida, during 1989. Species groups are identified by the following: BC = blue crab, BF = bait fishes, GS = grouper-snappers, ID = inshore demersals, IP = inshore pelagics, LB = lobsters, OD = offshore demersals, OP = offshore pelagics, SC = stone crab, SH = shrimps, and UM = unidentified miscellaneous fishes. Golden crab landings are included in the category "misc. invertebrates."

Species or complex	Weight (lb)	Group	Species or complex	Weight (lb)	Group
Amberjack	4,315	OP	Sea bass, mixed	327	ID
Bait Fish	246	BF	Shark	59,352	OP
Ballyhoo	23,204	BF	Shark fins	35	OP
Bluefish	38	IP	Sheepshead	120	ID
Bluerunner	813	BF	Hogfish	6,895	ID
Bonito (little tunny)	161	OP	Snapper, lane	833	GS
Bumper, Atlantic	94	BF	Snapper, mangrove	3,335	GS
Cobia	1,350	OP	Snapper, mutton	29,555	GS
Croaker	434	ID	Snapper, red	337	GS
Dolphin	32,704	OP	Snapper, silk	68	GS
Eels	20	ID	Snapper, vermilion	3,358	GS
Goggle eye or scad	1,510	BF	Snapper, yellowtail	23,443	GS
Grouper, black	33,255	GS	Snapper, mixed	11,438	GS
Grouper, gag	6,155	GS	Snapper, other	1,102	GS
Grouper, Nassau	40	GS	Spot	40	ID
Grouper, red	10,612	GS	Swordfish	811,896	OP
Grouper, scamp	194	GS	Tilefish, golden	320	OD
Grouper, snowy	939	GS	Tilefish, gray	800	OD
Grouper, Warsaw	764	GS	Triggerfish	2,289	ID
Grouper, yellowedge	74	GS	Tuna, bigeye	66,437	OP
Grouper, yellowfin	8	GS	Tuna, blackfin	457	OP
Jewfish	232	GS	Tuna, bluefin	2,530	OP
Grouper, mixed	527	GS	Tuna, skipjack	15	OP
Grouper, other	1,496	GS	Tuna, yellowfin	58,626	OP
Grunts	2,700	ID	Tuna, mixed	499	OP
Jack, crevalle	2,304	IP	Wahoo	759	OP
Jack, mixed	1,075	IP	Whiting	37	ID
Jack, other	392	IP	Misc. food fish	57,240	UM
Mackerel, king	25,848	OP	Misc. industrial fish	730	UM
Mackerel, Spanish	723	IP	**Total finfish**	**1,299,945**	
Menhaden (pogies)	218	IP	Crabs, blue (hard)	7,564	BC
Mojarra	697	ID	Crabs, stone, large	265	SD
Mullet, black	9	IP	Lobster, Spanish	225	LB
Mullet, silver	1,451	IP	Lobster, spiny	37,068	LB
Permit	1	IP	Octopus	163	ID
Pinfish	2	BF	Shrimp, pink	5,280	SH
Pompano	378	IP	Shrimp, bait	453	SH
Porgies	2,092	ID	Misc. invertebrates	4,458	OD
			Total invertebrates	**55,475**	
			Grand total	**1,355,421**	

February and June were least similar. About half (28 out of 66) of all possible unique pair-wise comparisons revealed significantly different assemblages (Table 3). These differences were usually due to changes in the proportion of landings contributed by swordfish and to the prevalence of lobster and baitfish.

The composition of the assemblage landed in a particular month varied considerably. The assemblage landed during any given month was significantly different from those of as few as two to as many as nine of the other eleven months. Assemblages of adjacent months were not significantly different, with the exception of July–August (owing to a sharp drop in swordfish landings and to a large increase in lobster landings at the beginning of the season) and September–October (owing to a sharp increase in swordfish landings and a general reordering of the dominance of other species) (Table 3). October was different from all months, except November and December, and July was different from all months, except June and September. January was different only

from July and October, whereas December was different only from February and July. Generally, there were significant differences between winter (large proportion of swordfish and other offshore pelagics) and late summer–fall (relatively small proportions of offshore pelagics with a mix of species from other groups) assemblages.

Table 2

Monthly diversity of commercial fisheries landings in Broward County, Florida, during 1989. H′ = Shannon-Wiener diversity; V′ = evenness; R = species richness.

Month	H′	V′	R
Jan	1.73	0.40	48
Feb	2.04	0.47	50
Mar	1.49	0.34	52
Apr	1.49	0.34	54
May	1.36	0.31	51
Jun	1.41	0.32	36
Jul	1.90	0.44	44
Aug	2.66	0.62	48
Sep	2.69	0.62	52
Oct	2.35	0.54	54
Nov	1.90	0.44	55
Dec	1.56	0.36	53
Mean	1.88	0.43	50

Classification

Cluster analysis classified trips on the basis of the similarity of the species assemblages landed. I used an artificial, but operational, system of general habitat associations and species complexes to classify species into eleven groups (Table 1). Groupers and snappers inhabit a wide variety of habitats (Smith, 1976; Robins et al., 1986) and were frequently landed together. They were assigned to their own group rather than limited to a single habitat. Similarly, bait fish often formed a unique cluster and thus a "bait fish" group was used. "Miscellaneous food/industrial fish (UM)" was a "catch all" group used by fishermen to report species that were not explicitly given an identification code by the MFIS. It usually included such species as angelfishes (Pomacanthidae), parrotfishes (Scaridae), butterfish (*Peprilus* spp.),

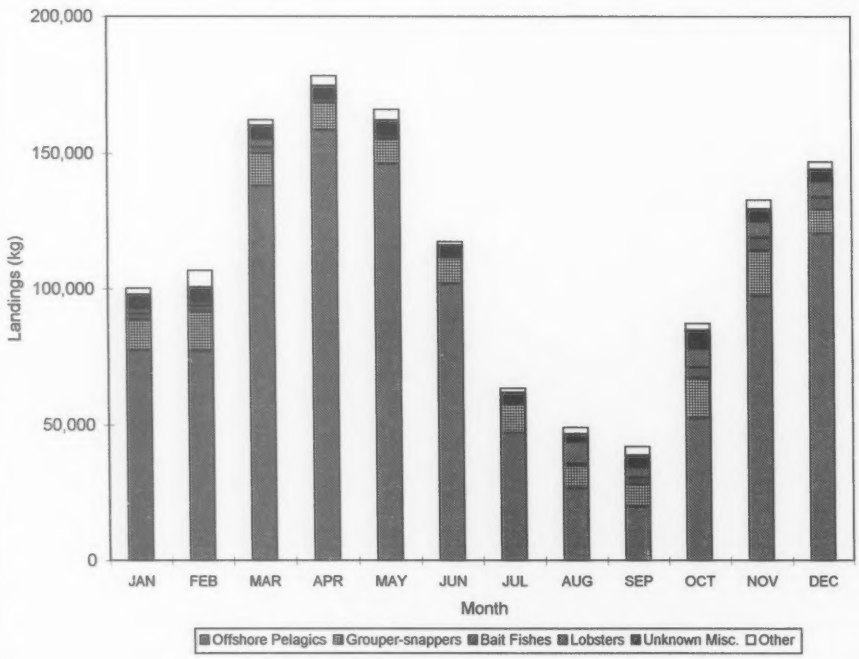


Figure 2

Total monthly landings in Broward County, Florida, during 1989 and the contribution of each species group. See Table 1 for species within each group. Each segment of each vertical bar represents the portion of total landings attributable to one of the five major groups (offshore pelagics, grouper-snappers, lobsters, bait fishes, and unknown miscellaneous fishes) or other species.

spadefish (*Chaetodipterus faber*), and tripletail (*Lobotes surinamensis*).

The persistence of each group in the harvest varied throughout the year. Offshore pelagics (OP, e.g. swordfish, *Xiphias gladius*) and tuna (*Thunnus* spp.), grouper-snapper (GS), bait fish (BF, e.g. ballyhoo, *Hemiramphus brasiliensis*), and unknown miscellaneous (UM) fishes occurred in each month. Lobsters (LB) occurred during each month of the open season (August–March) but declined steadily from the opening of the season. Blue crabs (BC, *Callinectes sapidus*) occurred in summer and fall (May–September and December). Inshore pelagics (IP, e.g. mullet, *Mugil* spp.) occurred in January, March, April, and August. Stone crabs (SC, *Menippe mercenaria*) and inshore demersals (ID, e.g. sheepshead, *Archosargus probatocephalus*) were landed in November and December. Shrimps (*Penaeus* spp.) occurred in February and April. Offshore demersals (OD, e.g. tilefish [Malacanthidae]) occurred only in July.

Offshore pelagics (OP) accounted for the largest proportion of landings in all months (Fig. 2). They also accounted for the majority of landings on most of the fishing trips from May through July, again in October and November. Groupers and snappers accounted for much of the remaining landings and dominated trips in January and December. Together the offshore pelagics (OP) and the grouper-snappers (GS) accounted for over 80% of landings in all months, except August, September, and October. The addition of lobster (LB) landings raises the totals for August and October to more than 80%. Inclusion of bait fish landings helps to account for more than 80% of September landings. Unknown miscellaneous (UM) fishes account for most of the remaining landings in each month.

Species associations

Despite the classification of landings (trip assemblages) into distinct groups of species assemblages, associations between individual species were weak. Less than 4% of the unique pair-wise comparisons of species occurrence in any given month were significant. One fourth to half of these accounted for more than 50% of the variation in their ranked abundances. Four associations accounted for more than 70% and only one association accounted for more than 80% of the variation in correlated species abundances. Roughly half of the significant associations were positive. However, most of these were between two uncommon (landed on less than ten trips per month) species. Only the swordfish-tuna association was consistently strong (r'>50%) and positive. Mutton snapper (*Lutjanus analis*) was positively associated with black grouper (*Mycteroperca bonaci*), mojarras (Gerreidae), and a number of other species, but these associations were not evident in every month and were usually weak (r'<50%). Only significant associations are considered in the following discussion.

Table 3

Dissimilarity and probabilities in comparing all pair-wise combinations of species assemblages landed in Broward County, Florida, during each month of 1989. The upper half matrix contains the dissimilarity values based on the Heterogeneity Ratio (HR), which is a measure of beta diversity. The lower half matrix contains the associated probabilities, generated by faunal similarity analysis (FAUNSIM), that the number of species observed to be common to each pair was less than that expected. Values in boldface are significant at the 0.05 level or greater.

	HR											
Month	1	2	3	4	5	6	7	8	9	10	11	12
1	—	1.057	1.073	1.107	1.084	1.179	**1.186**	1.143	1.104	**1.181**	1.112	1.112
2	0.07	—	1.071	**1.141**	**1.157**	**1.262**	**1.201**	1.118	**1.137**	**1.176**	1.109	**1.128**
3	0.53	0.40	—	1.069	1.101	**1.233**	**1.149**	1.087	1.050	**1.150**	1.089	1.089
4	0.80	**0.99**	0.43	—	1.098	**1.205**	**1.182**	1.101	1.064	**1.163**	**1.158**	1.105
5	0.38	**0.99**	0.67	0.75	—	1.160	**1.161**	**1.137**	1.098	**1.124**	1.081	1.082
6	0.71	**1.00**	**0.98**	0.87	0.47	—	1.161	1.159	**1.201**	**1.245**	**1.234**	1.212
7	**1.00**	**0.99**	**0.95**	**1.00**	**0.99**	0.62	—	1.157	1.137	**1.229**	**1.212**	**1.151**
8	0.93	0.80	0.66	0.73	**0.99**	0.66	1.00	—	1.063	**1.187**	1.130	1.089
9	0.80	0.97	0.33	0.51	0.86	**0.96**	0.83	0.10	—	**1.148**	**1.110**	1.090
10	**1.00**	**1.00**	**1.00**	**0.99**	**0.95**	**0.99**	**1.00**	**1.00**	**0.99**	—	1.115	1.095
11	0.76	0.88	0.75	**1.00**	0.58	**0.97**	**1.00**	**0.94**	**0.96**	0.86	—	1.070
12	0.77	**0.96**	0.75	0.84	0.50	0.90	**0.95**	0.66	0.88	0.67	0.44	—

FAUNSIM probability

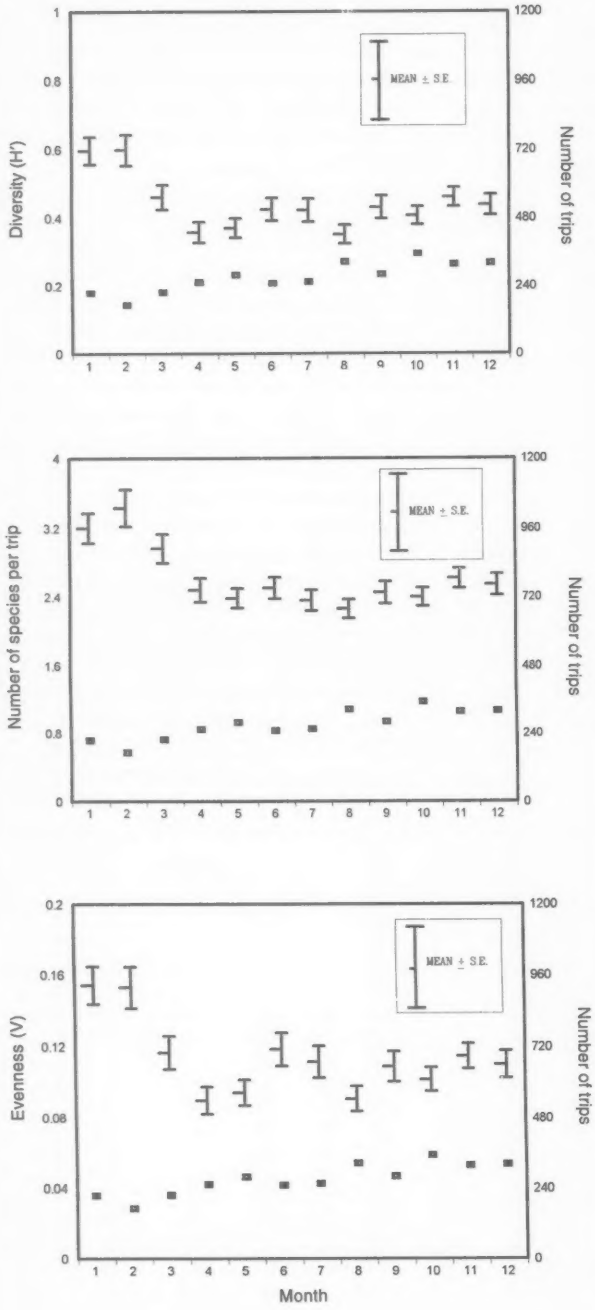


Figure 3

Monthly values of alpha diversity for trips landing fish in Broward County during 1989. Species richness, evenness, and the Shannon-Wiener information index are represented by these high-low graphs. Each horizontal tick mark indicates the mean value. Each vertical bar indicates one standard error. Solid rectangles represent the number of fishing trips associated with each high-low bar.

A strong, positive association between swordfish and both bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) existed in spring and fall. In December, the association between each of these tunas and swordfish accounted for over 70% of the variations in their landings. Swordfish showed significant negative associations with shark in the early part of the year and with dolphin (*Coryphaena hippurus*) throughout the year.

In 1989, all species of shark landed were reported under the unspecific "mixed shark" code. At least eleven species of shark are landed throughout the state, but blacktip shark (*Carcharhinus limbatus*), sandbar shark (*Carcharhinus plumbeus*), and shortfin mako (*Isurus oxyrinchus*) are most common in the landings from southeast Florida (Brown[7]). Shark landings were negatively correlated with all significant associates in Broward County. There were strong negative associations between sharks and both groupers and snappers throughout most of the year and between sharks and dolphins in spring and fall.

Dolphin landings were negatively correlated with all significant associates except for a few rare positive associations with tunas in mid-summer. They showed strong negative associations with groupers in the early part of the year and with snappers throughout most of the year.

King mackerel (*Scomberomorus cavalla*) is a migratory species and a seasonal member of the offshore pelagics (OP) group (Manooch, 1979; Collette and Russo, 1984). Those caught in the waters off Broward County are considered part of the Atlantic stock from 1 April until 1 November, when they become part of the Gulf–Atlantic stock. The fishery on the Gulf–Atlantic stock is quota-regulated in Florida and usually closes in late December or early January. In 1989, king mackerel landed in Broward County displayed strong, negative associations with dolphin, groupers, and snappers. It also was rarely associated with baitfishes, lobsters, and other offshore pelagics.

Spiny lobster (*Panulirus argus*) landings in Florida occur only during the open sea-

[7] Brown, S. T. 1994. Florida Marine Research Inst., Florida Dep. Environmental Protection, 100 8th Ave SE, St. Petersburg, FL 33701. Personal commun.

son (6 August through 31 March). Broward County lobster landings were consistently negatively associated with yellowtail snapper (*Ocyurus chrysurus*) and "mixed snapper." They were positively associated with grunts (Haemulidae) and "other groupers" in December. A strong positive association with Spanish lobster (*Scyllarides aequinoctialis*) occurred in October.

Black grouper occurred with nine other species and UM. It was negatively associated with lobsters and members of the offshore pelagics group, especially dolphin, king mackerel, and shark. There was a consistent positive association only with mutton snapper.

Hogfish (*Lachnolaimus maximus*) occurred with a dozen other species and UM. This species showed a strong and consistent negative association with sharks and sporadic positive associations with mutton snapper in summer and fall.

Mutton snapper was significantly associated with the largest number of other species (25) but showed consistent associations with only a few. There was a consistent negative association with sharks and dolphin throughout most of the year. Landings of mutton snapper were positively related to those of groupers and mojarra (Gerreidae) in the latter half of the year. This species was frequently associated with hogfish in summer and fall.

Yellowtail snapper was also significantly associated with a large number of other species (18), but showed few consistent associations. Positive associations were rare but negative associations with dolphin, shark, and spiny lobster were common.

Species assemblages

Seasonal differences suggested by changes in diversity and similarity were evident in the species assemblages landed each month (Table 4). Offshore pelagic species dominated Broward County landings in 1989 (Fig. 2). Swordfish, shark, and dolphin were listed on at least ten trip tickets every month. Swordfish dominated annual landings as well as those for each month; it accounted for 60% of annual landings (Fig. 4) and more than 50% of landings in all months except August, September, and October. Other offshore pelagics accounted for 18% of annual landings (Fig. 4). Bigeye and yellowfin tunas occurred commonly in nine or more months but were uncommon in the summer. King mackerel occurred commonly in all months except January through March, when the fishing season was closed. Spiny lobster accounted for less than 3% of the annual landings (Fig. 4) but made a large contribution to the landings in the first part of the open season (August: 15% of the landings) and tapered off throughout the fall. Groupers and snappers accounted for more than 6% of the annual landings, but only black grouper, mutton snapper, and yellowtail snapper accounted for more than 1% of annual landings each (Fig. 4). Black grouper, hogfish, mutton snapper, yellowtail snapper, and mixed snappers occurred commonly in every month. Red grouper (*Epinephalus morio*) was common every month, except January. Gag (*Mycteroperca microlepis*) was common only in April, and "other grouper" in winter and September. Unknown mis-

Table 4

Species contributions (as a percentage) to monthly landings in Broward County, Florida, during 1989. (See Table 1 for group definitions.)

Group	Species or complex	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
GS	Black grouper	3.0	4.3	2.0	1.8	1.7	2.0	3.7	3.8	4.6	3.4	1.6	1.7
	Mutton snapper	1.4	2.3	0.7	0.6	0.9	2.2	3.3	2.5	5.1	5.9	5.1	1.3
	Yellowtail snapper	3.2	2.0	1.0	0.7	0.9	2.2	2.9	4.8	5.2	2.3	1.6	0.4
	Mixed snapper	0.7	0.5	0.3	0.4	0.4	0.6	2.0	1.5	2.1	2.4	1.3	0.7
LB	Lobster	2.0	1.4	1.9	0.0	0.0	0.0	0.0	16.5	9.0	7.8	4.5	4.0
OP	Bigeye tuna	5.0	8.3	5.4	1.9	3.2	2.7	1.8	5.8	1.1	6.8	7.6	7.7
	Dolphinfish	1.8	1.7	1.6	1.0	1.4	5.4	9.7	8.8	4.7	2.0	0.5	0.7
	King mackerel	0.0	0.0	0.0	9.0	1.7	0.4	0.7	2.3	0.7	1.8	0.6	1.0
	Shark	4.3	3.4	5.8	5.7	6.6	4.7	2.3	4.1	5.2	4.0	1.9	2.4
	Swordfish	62.8	53.5	68.2	67.2	71.4	68.2	54.5	25.4	29.5	38.6	55.2	65.2
	Yellowfin tuna	2.3	3.3	1.8	3.6	3.3	5.2	4.4	8.0	5.7	6.8	7.3	4.8
UM	Misc. food fish	5.0	5.0	3.1	2.7	3.3	3.7	6.6	5.7	10.6	7.7	3.4	3.0
	Other species	12.3	13.1	13.2	11.1	10.4	5.8	8.7	14.0	13.6	8.3	12.0	8.3

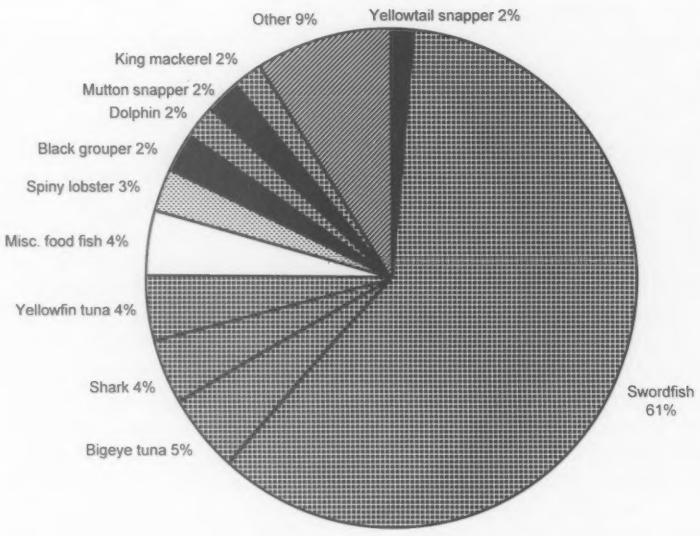


Figure 4

Fish species assemblage, based on the total weight of commercial landings in Broward County during 1989. Pie slices shaded with a crosshatch pattern identify species classified as offshore pelagics (OP), those shown as black identify species classified as members of the grouper-snapper (GS) complex, those shown as white identify unknown miscellaneous fishes (UM), those with a dot pattern identify lobsters (LB) landings, and those with a diagonal line pattern identify other species.

cellaneous food fish accounted for 4.2% of Broward County landings in 1989.

Discussion

The diversity of the Broward County harvest in 1989 was relatively low compared with that of a natural marine fish community in Florida. The tropical reef communities of the Florida Keys are some of the richest in the world; more than 500 fish species have been reported on Alligator Reef alone (Starck, 1968). Species-rich fish communities, however, are not restricted to coral reef habitats. Gilmore (1977) and Gilmore and Hastings (1983) reviewed fish collections associated with the Indian River system. They were able to compile a list of 685 species and projected that more than 700 species should be found in that region. The species richness in those studies varied considerably (26–275 species) from habitat to habitat. Grass flats, inlets, and offshore reefs had the richest fish faunas (>200 species). From offshore continental-shelf habitats alone, more than 170 species were found. Anderson and Gehringer (1965) collected 64 species of fish in 94 hours of trawling over the continental shelf of the Indian River region. Herrema's (1974) marine fish collections from off parts of Broward and Palm Beach counties included 583 species, although many of these are not commercially harvested or are taken in limited number for aquarium collectors. Nevertheless, 76 species of fish and shellfish commercially landed from more than 3,000 fishing trips is a poor representation of the fauna known to be present.

This low species richness is, of course, a reflection of the selectivity of commercial fishing efforts. Only certain sizes of the vulnerable species are available to the gear and only a fraction of these are captured. However, it is unlikely that a catch will be restricted to the two or three species that were landed per trip, on average (Fig. 3) (Fisher et al., 1943). Fishermen keep only the species and sizes that have a market value, discarding all others. The clear seasonal changes in the assemblages landed reflects a balance between changing availability of different fish species to the gear and market values of the various species. Presumably, the commonly landed species were the most valuable. Offshore pelagic species, especially swordfish, were clearly targeted in 1989, as were groupers and snappers. The low summer

landings of offshore pelagics may reflect a decrease in availability as swordfish moved out of the fishing area (Hoey[8]) or a decline in market value, or both. An examination of catch records showed no evidence that fishermen who harvest offshore pelagics had switched to another fishery. However, the increase in landings of lobsters by some fishermen who target grouper-snappers and inshore demersals is indicative of a shift to the more valuable lobster fishery when the season opens.

The grouping of trips into distinct clusters that roughly correspond to different habitats indicates a structure among the fishermen, based on what they target. The use of specific gear and fishing sites restricts the diversity of the catch. The fisherman's ability to use different gear (sometimes on the same trip) and visit different sites is a key characteristic of Florida's fisheries. Twenty-five types of gear were registered by Broward County fishermen in 1989. Such unusual combinations as longlining for swordfish and pulling traps for lobster commonly occur on the same trip. Six hundred and ninety-eight of the 907 fishermen registered rod-and-reel as one of the gear types they possessed (not necessarily used). Each fisherman may register more than one type of gear. The fishing potential of each gear is also different. Only 72 fishermen registered surface long lines, but those 72 lines had a total of 29,445 hooks.

Florida also requires special licenses for use of certain gear and for landing some species. Two hundred and eighty-two lobster (crawfish) licenses were issued to Broward County fishermen in 1989 (207 fishermen registered a total of 32,433 traps). Other special licenses included: blue crab (76), stone crab (123), shrimp (2), and purse seine (1).

Species groups identified by the cluster analysis (Table 1) correspond to those that are vulnerable to different gear types. Species in the offshore pelagic group are caught in offshore surface waters with hook-and-line and surface long lines (Berkely et al., 1981). Most of the common groupers and snappers are caught in shallow, nearshore or shelf waters with hook-and-line. Bait fish are found in all surface waters and are caught with small purse seines and lampara nets. Lobsters and stone crabs are found offshore, whereas blue crabs are harvested from inshore and estuarine waters. All three are caught in traps, but lobster are also landed with shrimp in trawls. By having more than one gear type, a fisherman can simply rerig his vessel (and possibly work a different site) and partake of a completely different component of the fishery.

The general negative associations among species is another indication of the selective behavior of commercial fishermen. Since the ideal catch for a fisherman is a monocrop of the most valuable targeted species available, landed assemblages are likely to be as close to that ideal as possible. The catch is sorted and filtered such that the vessel's hold capacity is filled with the greatest amount of the most valuable species caught by the gear (Gulland, 1983). Thus, one would expect some trips to be monospecific, others to include a minimum number of other species. Without detailed information on discards and fisherman behavior, it is difficult to determine if negative associations represent an ecological condition whereby the two species avoid each other (or have different, but overlapping habitat requirements) or if they are an artifact of gear selection and fisherman behavior. Most likely they are the result of a combination of these factors.

The selectivity of the commercial fishing process and the nonrandom sampling of the natural environment makes it extremely difficult to use commercial landings data to gain insight into the natural fish community of a region. The commercial data provide only one component of the mortality affecting a fish community. Landings by recreational fishermen can be substantial (Essig et al., 1991) but are often unavailable. Moreover, fish discarded at sea often represent the largest component of fishing mortality in a region (FAO, 1973); the market values that drive the selection process are often not available with the landings data. Nonrandom spatial and temporal distribution of harvest can yield only biased estimates of fish population sizes, and the extent of that bias cannot be determined.

Conclusions

There was clear structure to the commercial fishery harvest in Broward County during 1989. The low diversity, classification of trips into habitats fished, and negative species associations were clear indications of the selectivity in the system. A rich variety of species were landed by the fishery as a whole, but fishermen focused individual trips on a restricted subset of these species. The multispecies nature of the fishery and the potential for fishermen to exploit different components of the fishery are important features and should be carefully considered when forming management strategies.

These commercial data tell us little about the natural fish community from which the harvest was

[8] Hoey, J. J. 1985. Addendum to the source document for the swordfish fishery management plan, Part I. Prepared by and available from: South Atlantic Fishery Management Council, 1 South Park Circle, Suite 306, Charleston, SC, 132 p.

drawn. All that can be stated with certainty about the biological community is the tautology: the fish that were landed were present at the site where the gear was deployed and were available to the gear used at the time. The biases introduced by the selectivity of this system obscure events in the natural system and provide little insight into the changes in the fish community. However, these data do show a clear structure of the harvest due to fishing behavior and how that structure changes seasonally. The causes of those changes remain unclear. To address this problem, more effort in quantifying discards, recreational fishing mortality, and natural variability is needed, as well as a better understanding of the accessibility and economics driving the social system.

Acknowledgments

I would like to thank R. G. Muller, F. S. Kennedy, and J. R. O'Hop for their guidance and editorial comments. Special thanks go to E. Irby for providing me with valuable insight into the harvest of offshore pelagic species. I am also indebted to J. Quinn for his extensive editorial comments on this document.

Literature cited

Anderson, W. W., and J. W. Gehringer.
1965. Biological-statistical census of the species entering fisheries in the Cape Canaveral area. U.S. Fish Wildlife Serv., Spec. Sci. Rep.-Fisheries 514, 79 p.

Beddington, J. R.
1986. Shifts in resource populations in large marine ecosystems. *In* K. Sherman and L. M. Alexander (eds.), Variability and management of large marine ecosystems, p. 9–18. Am. Assoc. Adv. Sci. (AAAS) selected symposium 99.

Beddington, J. R., and R. M. May.
1982. The harvesting of interacting species in a natural ecosystem. Scientific American 247:62–69.

Berkely, S. A., E. W. Irby Jr., and J. W. Jolly Jr.
1981. Florida's commercial swordfish fishery: longline gear and methods. Mar. Advis. Bull. MAP-14, Florida Cooperative Extension Service, Florida Sea Grant Program.

Bohnsack, J. A., D. E. Harper, and D. B. McClellan.
1994. Fisheries trends from Monroe county, Florida. Bull. Mar. Sci. 54:982–1018.

Collette, B. B., and J. L. Russo.
1984. Morphology, systematics, and biology of the Spanish mackerels (*Scomberomorus*, Scombridae). Fish. Bull. 82:545–646.

Cushing, J.
1961. On the failure of the Plymouth herring fishery. Mar. Biol. Assoc. U.K. 41:899–916.

Essig, R., J. F. Witzig, and M. C. Holliday.
1991. Marine recreational fishery statistics survey, Atlantic and Gulf coasts, 1987–1989. Current fisheries statistics number 1804. U.S. Dep. Commer., NMFS, NOAA, Silver Spring, MD, 363 p.

Fable, W. A., Jr.
1990. Summary of king mackerel tagging in the southeastern USA: mark-recapture techniques and factors influencing tag returns. Am. Fish. Soc. Symp. 7:161–167.

Fisher, R. A., A. S. Corbet, and C.B. Williams.
1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Animal Ecology 12:42–58.

FAO (U.N. Food and Agriculture Organization).
1973. Report of the expert consultation on selective shrimp trawls; Ijmuiden, The Netherlands, 12–14 June 1973. FAO Fishery Rep. 139, 71 p.

Freund, J. E.
1970. Statistics, a first course, 2nd ed. Prentice-Hall, New York, NY, 340 p.

Gilmore, R. G., Jr.
1977. Fishes of the Indian River lagoon and adjacent waters, Florida. Bull. Fla. State Mus., Biol. Sci. 22:101–148.

Gilmore, R. G., and P. A. Hastings.
1983. Observations on the ecology and distribution of certain tropical peripheral fishes in Florida. Fla. Sci. 46:31–51.

Gulland, J. A.
1983. Fish stock assessment: a manual of basic methods. Ch. 1: Introduction, p. 1–20. John Wiley & Sons, New York, NY.

Herrema, D. J.
1974. Marine and brackish water fishes of southern Palm Beach and northern Broward Counties, Florida. M.S. thesis, Florida Atlantic Univ., Boca Raton, FL, 179 p.

Idyll. C. P.
1973. The anchovy crisis. Scientific American 228:22–29.

Kobayashi, S.
1987. Heterogeneity ratio: a measure of beta-diversity and its use in community classification. Ecol. Res. 2:101–111.

Manooch. C. S.
1979. Recreational and commercial fisheries for king mackerel, *Scomberomorus cavalla*, in the South Atlantic Bight and Gulf of Mexico, U.S.A. *In* E. L. Nakamura and H. R. Bullis Jr. (eds), Proceedings of the colloquium on the Spanish and king mackerel resources of the Gulf of Mexico, p. 33–46. Gulf States Mar. Fish. Comm. 4.

McKenna, J. E., Jr., and S. B. Saila.
1991. Application of an objective method for detecting changes in fish communities: Samar Sea, Philippines. Asian Fish. Sci. 4:201–210.

Moe, M. A.
1991. Lobsters. Florida, Bahamas, the Caribbean. Chapter 6: The commercial fishery, balancing effort and conservation, p. 373–451. Green Turtle Publications, Plantation, FL.

Nakamura, E. L. and H. R. Bullis Jr. (eds.)
1979. Proceedings of the colloquium on the Spanish and king mackerel resources of the Gulf of Mexico, no. 4; twenty-eighth annual spring meeting of the Gulf States Marine Fisheries Commission, Brownsville, Texas, March 16, 1978.

Newlin, K. (ed.)
1991. Fishing trends and conditions in the Southeast Region 1990. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC-292, 84 p.

Pielou E. C.
1977. Mathematical ecology. Chapter 20: The classification of communities, p. 312–331. John Wiley & Sons, New York, NY.

Raup, D. M., and R. E. Crick.
1979. Measurement of faunal similarity in paleontology. J. Paleontology 53:1213–1227.

Robins, C. R., G. C. Ray, and J. Douglass.
1986. A field guide to Atlantic coast fishes of North America. Houghton Mifflin Company, Boston, MA, 354 p.

SAS Institute.
1985. SAS user's guide: statistics, 5th ed. SAS Institute Inc., Box 8000, Cary, NC 27511-8000, 956 p.

Sissenwine, M. P.
1986. Perturbation of a predator-controlled continental shelf ecosystem. *In* Sherman K. and L. M. Alexander (eds.), Variability and management of large marine ecosystems, p. 55–85. AAAS selected symposium 99.

Shannon, C. E., and W. Weaver.
1949. The mathematical theory of communication. Univ. Illinois Press, Urbana, IL, 125 p.

Smith, G. B.
1976. Ecology and distribution of Eastern Gulf of Mexico reef fishes. Florida Marine Research Publications 19, 78 p.

Starck, W. A. II.
1968. A list of fishes of Alligator Reef, Florida, with comments on the nature of the Florida reef fish fauna. Undersea Biology 1:4–40.

Year-class twinning in sympatric seasonal spawning populations of Atlantic herring, *Clupea harengus*

Ian H. McQuinn

Division Poissons et Mammifères marins, Ministère des Pêches et des Océans
Institut Maurice Lamontagne, C.P. 1000, 850 Route de la Mer
Mont-Joli (Québec), Canada G5H 3Z4

E-mail address: I_McQuinn@qc.dfo.ca

Abstract.—This study compared the hatching season and the actual spawning season of spring- and autumn-spawning herring in the northern Gulf of St. Lawrence as determined by otolith characteristics and maturity stages, respectively, to measure the crossover between the two spawning populations. The growth characteristics of two cohorts that showed significant crossover were contrasted with those of a cohort that did not. It was concluded that variable juvenile growth does influence the adoption of the season of first spawning in these populations, and therefore the progeny of a given seasonal-spawning population may recruit to a local population that has a different reproductive season. It was also shown that the twinning of year-class strength can be explained by the crossover of a large number of individuals from one seasonal spawning population to another. The data presented indicate that the spawning season that is established at the time of first maturation is maintained for the remainder of adult life. The present study therefore does not support the concept of discrete sympatric seasonal-spawning populations in Atlantic herring.

Manuscript accepted 7 August 1996.
Fishery Bulletin 95:126–136 (1997).

The current theory on Atlantic herring population structure, as it relates to sympatric spring- and autumn-spawning herring, considers them to be discrete populations with independent life histories (Iles and Sinclair, 1982). This concept has largely been based on evidence of significant homing precision to spawning grounds as revealed by tag returns (Hourston, 1982; Wheeler and Winters 1984, a and b; Stevenson et al.[1]; Hart et al.[2]; Stobo[3]) and on studies that have noted significant differences in meristic and morphometric measurements, such as fin-ray counts and otolith characteristics (Messieh, 1972; Parsons, 1973; Postuma, 1974), as well as in life history parameters, such as mean fecundities (Baxter, 1959; Messieh, 1976).

However, several observations are difficult to explain within the discrete population concept: 1) typical spring-type otoliths are often found in autumn-spawning herring and vice versa (Messieh, 1972; Aneer, 1985); 2) "twinning" of recruitment strength between spring- and autumn-spawning year classes (see below); and 3) the lack of genetic divergence between seasonal spawning populations as demonstrated from numerous electrophoretic and mtDNA studies (Grant, 1984; Kornfield and Bogdanowicz, 1987; Safford and Booke, 1992). In light of the conflicting evidence for stock discreteness, an alternative concept has been proposed whereby seasonal spawning populations are seen as subunits of a larger population, within which there exists a "dynamic balance" characterized by extensive gene flow (Smith and Jamieson, 1986).

Otolith characteristics and maturity stages have been used for many decades to determine the spawning affinity of individual herring from sympatric seasonal-spawning populations. Maturity stages are the preferred method for determining the actual spawning season of mature herring because the state of maturation can be used reliably to ascertain the spawning season throughout the year (McQuinn, 1989). On the other hand, otolith characteristics, being related mainly to environmental conditions at birth, are used to determine the hatching sea-

[1] Stevenson, J. C., A. S Hourston, K. J. Jackson, and D. N. Outram. 1952. Results of the West Coast of Vancouver Island herring investigation, 1951–52. Report of the British Columbia Provincial Fisheries Department, Victoria, British Columbia, Canada, p. 57–87.

[2] Hart, J. L., A. L. Tester, and J. L. McHugh. 1941. The tagging of herring (*Clupea pallasii*) in British Columbia: insertions and recoveries during 1940–41. Report of the British Columbia Provincial Fisheries Department, Victoria, British Columbia, Canada, p. 47–74.

[3] Stobo, W. T. 1982. Tagging studies on Scotian shelf herring. Northwest Atlantic Fisheries Organization (NAFO) Research SCR Document 82/IX/108. Ser. No. N617, 16 p. P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

son (Einarsson, 1951; Postuma and Zijlstra, 1958; Messieh, 1972). The comparison of hatching season with spawning season as determined by these two methods, respectively, thus provides us with a rare opportunity to study the reproductive interactions between sympatric seasonal-spawning herring populations.

As with most herring populations, herring from western Newfoundland (Canada) are characterized by the periodic appearance of very large year classes followed by several years of relatively poor recruitment. In addition, the sympatric seasonal-spawning populations in eastern Canadian waters often show year-class twinning (Winters et al., 1986; de Lafontaine et al., 1991). This phenomenon is most evident when a strong autumn-spawning year class of a given year coincides with a strong spring-spawning year class of the following year. Twinning is relatively common with seasonal-spawning populations but does not always occur. It is also true that year-class twinning rarely occurs between successive spring- and autumn-spawning year classes of the same year.

Winters et al. (1986) showed a weak, though significant, relationship between year-class strength (natural log scale) of autumn-spawning herring in eastern Newfoundland and that of spring spawners of the following year. An example where year-class twinning occurred in the western Newfoundland herring populations is with the 1979 autumn-spawning and 1980 spring-spawning year classes, both of which were very large (McQuinn and Lefebvre[4]). However, the 1982 spring-spawning year class was also very large but had no large autumn-spawning twin in 1981. Again we observed twinning with the 1986 and 1987 autumn- and spring-spawning year classes. What then are the characteristics that distinguish these year classes and that might explain why twinning occurred in 1979–80 and 1986–87, but not in 1981–82?

Year-class twinning was first reported in herring by Einarsson (1952), who termed it "year-class strength parallelism." He speculated that favorable oceanographic and feeding conditions occurring from the fall of one year until the following summer resulted in a parallelism in larval survival between the two spawning populations. However, an alternative explanation is that year-class twinning is simply a consequence of straying between sympatric spring- and autumn-spawning populations, i.e. significant numbers of individuals from a large cohort of one seasonal-spawning population subsequently spawn in the other season, creating a strong year class in both populations. Jean[5] and Graham (1962) suggested that the determination of spawning season of sympatric herring populations may be influenced by juvenile growth rates. Winters et al. (1986) presented data in support of their hypothesis that faster-growing spring-spawned juveniles may become autumn-spawners and conversely that slow-growing autumn-spawned juveniles may spawn in the spring. The objective of the present study is to use the otolith characteristics and maturity stage methods to establish whether indeed juvenile growth rates (as represented by size at age) have an effect on the determination of the onset of first maturation and thus the establishment of spawning season in Atlantic herring.

Materials and methods

Data for this study were collected from the west coast of Newfoundland herring fishery from 1982 to 1990 (after 1990 otolith characteristics of mature herring were no longer determined by our agers). Samples were frozen and shipped to the Fisheries and Oceans laboratories for detailed analyses. Basic biological data (total length, total weight, gonad weight, and otolith characteristics, as well as the number of winter rings from which age was determined) were recorded for all specimens.

The hatching season was ascertained for each fish from otolith characteristics by applying the standard criteria (the size and type—opaque or hyaline—of the nucleus) developed by the Canadian Atlantic Fisheries Scientific Advisory Committee as described by Cleary et al.[6] These criteria were developed from the rationale that rapid growth in the first summer of spring-spawned herring results in a small opaque otolith nucleus. Conversely, the slow first-winter growth of autumn-spawned herring results in a large hyaline otolith center and the first-winter ring is formed only in their second year (Jakobsson et al., 1969; Postuma, 1974). Although the assignment of hatching season is determined subjectively from these criteria, consistency between agers has been shown to be relatively high. A comparative study was

[4] McQuinn, I. H., and L. Lefebvre. 1994. An assessment of the west coast of Newfoundland (NAFO division 4R) herring resource up to 1993. Department of Fisheries and Oceans (DFO) Res. Doc. 94/43, 48 p. Atlantic Stock Assessment Secretariat, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

[5] Jean, Y. 1956. A study of the spring and fall spawning herring *Clupea harengus* L. at Grande-Rivière, Bay of Chaleur, Québec. Contribution 49 of the Department of Fisheries, Québec, Québec, Canada, 76 p.

[6] Cleary, L., J. J. Hunt, J. Moores, and D. Tremblay. 1982. Herring aging workshop; St. John's, Newfoundland, March 1982. Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Res. Doc. 82/41, 10 p. CAFSAC, Department of Fisheries and Oceans, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

conducted involving our ager and several other experienced otolith readers who used otoliths collected from throughout the Gulf of St. Lawrence (Savard and Simoneau[7]). This study showed a high agreement between two agers from our laboratory in Quebec (87%) and agers from the southern Gulf of St. Lawrence and eastern Newfoundland (75 and 76%, respectively) in the assignment of seasonal-spawning type from otoliths.

The actual spawning season of the mature individuals was determined from the stage of sexual maturity of each individual by using a temporal gonadosomatic index model (McQuinn, 1989). This model identifies the spawning season by first determining the maturity stage from the ratio of the gonad weight to a power function of the total length and by relating this state of maturation to the month of capture. Although spawning can occur from April to October, the vast majority of spring herring spawn in May and June, whereas the autumn herring spawn mainly from mid-August to September (Haegele and Schweigert, 1985). The date separating the two spawning seasons was arbitrarily chosen to be 1 July, as relatively little spawning occurs in late June and early July (McQuinn, 1989; Cleary et al.[6]).

Throughout this paper, a distinction is made between the number of rings read from the otoliths and the actual age of the fish because age determination depends upon whether an individual is assigned as a spring spawner or an autumn spawner. Most autumn-spawning herring (August–November) do not produce a winter ring on the otolith in their first year of life (Einarsson, 1951; Jakobsson et al., 1969; Rosenberg and Palmen, 1982; Hunt et al.[8]). The formation of the winter ring takes place between October and April–May in metamorphosed juveniles

[7] Savard, L., and M. Simoneau. 1983. Lecture comparative d'otolithes de hareng et utilisation des stades de maturité sexuelle pour l'attribution du groupe reproducteur. Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Res. Doc. 83/86, 28 p. Department of Fisheries and Oceans, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

[8] Hunt, J. J., L. S. Parsons, J. E. Watson, and G. H. Winters. 1973. Report of the herring ageing workshop; St. Andrews, New Brunswick, 11–13 December 1972. International Commission for the Northwest Atlantic Fisheries (ICNAF) Res. Doc. 73/2, Ser. 2901, 2 p. ICNAF, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

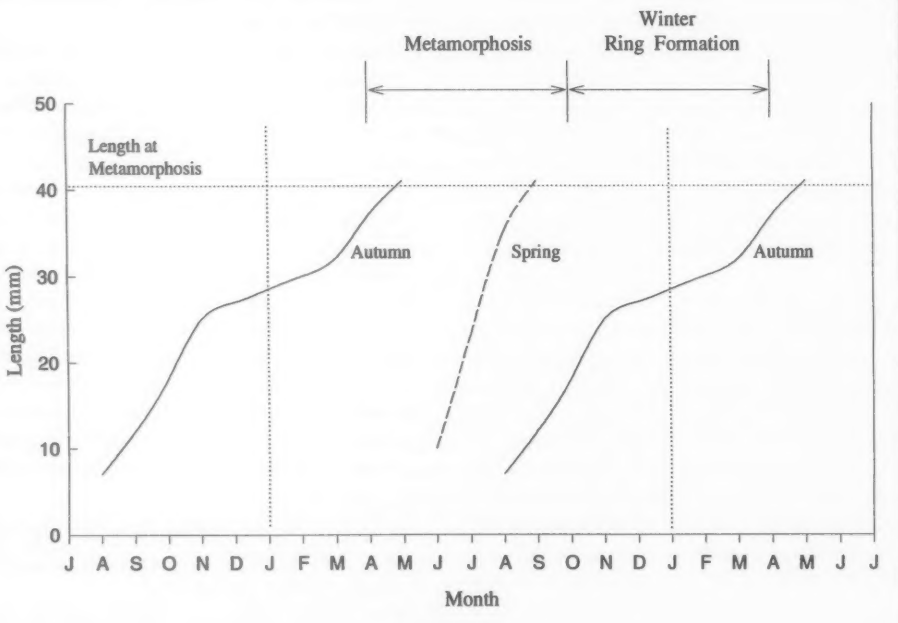


Figure 1

Generalized depiction of larval growth rates, timing of metamorphosis (from Sinclair and Tremblay, 1984), and otolith winter ring formation (from Messieh[9]) for spring- and autumn-hatched herring.

(Postuma, 1974; Messieh[9]), whereas newly hatched autumn spawners are still larvae (Fig. 1). Thus to assign correctly the age of a herring hatched in the autumn, one must add one year to the number of winter rings read from the otolith. Because spring-hatched herring metamorphose before their first winter and thus produce a winter ring in their first year, their proper age is equal to the number of winter rings. However, for any spring-hatched herring that subsequently reproduces in the autumn, its spawning season would be considered autumn with the maturity-stage method, and one year would be added to the number of rings read from the otolith. Following the same logic in reverse, if an autumn-hatched individual subsequently spawned in the spring, a year would not be added to the number of rings read from the otoliths and it would be assigned an age that was one year younger than its actual age. Therefore, the number of rings will be used when comparing the biological characteristics for a given age between an autumn-spawning year class with the spring-spawning year class of the following year.

[9] Messieh, S. N. 1974. Problems of ageing Atlantic herring (*Clupea harengus harengus* L.) in the ICNAF area. International Commision for the Northwest Atlantic Fisheries (ICNAF) Res. Doc. 74/59, Ser. 3274, 6 p. ICNAF, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

Results

The proportion of spring- and autumn-hatched herring was estimated from the mature members of the 1979–80, 1981–82 and 1986–87 autumn- and spring-spawning year classes, respectively (Table 1). According to their otolith characteristics, the vast majority (>90%) of the 1980 and 1982 spring-spawning herring were also spring hatched. This pattern is consistent from age 3 through age 5 (age=no. of rings). However, a large percentage of the 1979 (40%) and 1981 (77%) autumn-spawning herring were also spring hatched, as judged from their otolith characteristics. Therefore, in both situations, there was a significant crossover from the strong spring-hatched cohort to the autumn-spawning population, in comparison with the number of autumn-hatched individuals. However, because the resulting 1979 autumn-spawning year class was also large, whereas the 1981 autumn-spawning year-class was not, this

Table 1

Percentage of autumn- and spring-hatched herring that became mature autumn and spring spawners within the 1979, 1981, and 1986 autumn-spawning and within the 1980, 1982, and 1987 spring-spawning year classes off western Newfoundland (age is expressed as the number of otolith rings—see text).

		1979 autumn-spawning year class			1980 spring-spawning year class		
Year	No. of rings	Autumn-hatched (%)	Spring-hatched (%)	*n*	Spring-hatched (%)	Autumn-hatched (%)	*n*
1983	3	34.5	65.5	712	90.6	9.4	402
1984	4	55.6	44.4	1923	92.3	7.7	1438
1985	5	60.4	39.6	1760	92.4	7.6	2590
		1981 autumn-spawning year class			1982 spring-spawning year class		
Year	No. of rings	Autumn-hatched (%)	Spring-hatched (%)	*n*	Spring-hatched (%)	Autumn-hatched (%)	*n*
1985	3	54.4	45.6	68	92.2	7.8	192
1986	4	30.7	69.3	140	95.2	4.8	481
1987	5	22.6	77.4	186	97.2	2.8	966
		1986 autumn-spawning year class			1987 spring-spawning year class		
Year	No. of rings	Autumn-hatched (%)	Spring-hatched (%)	*n*	Spring-hatched (%)	Autumn-hatched (%)	*n*
1990	3	86.0	14.0	57	68.8	31.2	32

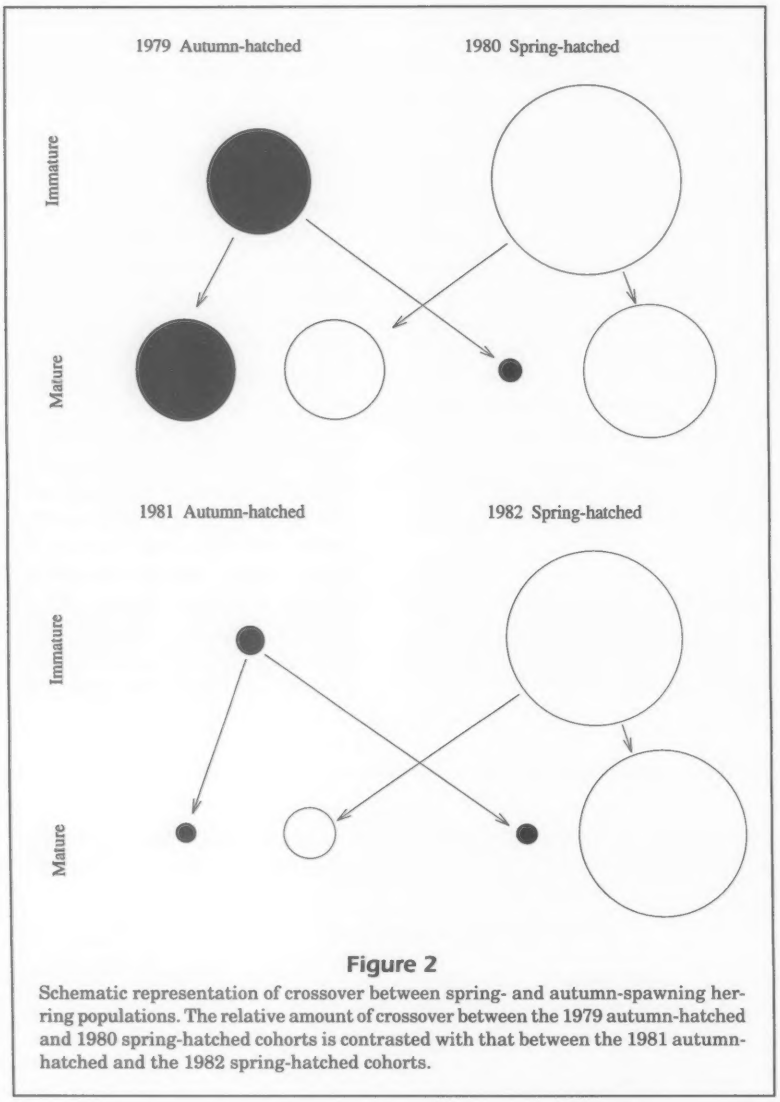


Figure 2

Schematic representation of crossover between spring- and autumn-spawning herring populations. The relative amount of crossover between the 1979 autumn-hatched and 1980 spring-hatched cohorts is contrasted with that between the 1981 autumn-hatched and the 1982 spring-hatched cohorts.

crossover was much less important in absolute terms in the latter (Fig. 2). This pattern is different for the 1986 and 1987 autumn- and spring-hatched cohorts (Table 1). There appears to have been a larger net migration (31%) from the autumn-hatched cohort towards the spring-spawners at age 4 (age=no. of rings + 1). Furthermore, the 1979 autumn-spawning year class showed a trend of a decreasing proportion of spring-hatched individuals from age 4 to 6 as more autumn-hatched individuals matured and recruited to the year class (Table 1). Conversely, the 1981 autumn-spawning year class showed an increasing percentage of spring-hatched individuals with age owing to the overwhelming dominance of the large 1982 spring-hatched cohort compared with the small 1981 autumn-hatched cohort (Fig. 2).

I have also summarized the mean lengths and standard deviations of the immature 1980 and 1982 spring-hatched cohorts to compare their average growth characteristics prior to their first spawning (Table 2). Although the means are similar at similar ages, the standard deviations are quite different, those for the 1980 cohort being 44% to 79% greater than the 1982 cohort from age 2 to age 3. The difference between the two cohorts is even more obvious when their length-frequency distributions at age 3 are compared (Fig. 3, A and B). The length distribution of the 1980 cohort is wider and bimodal. The

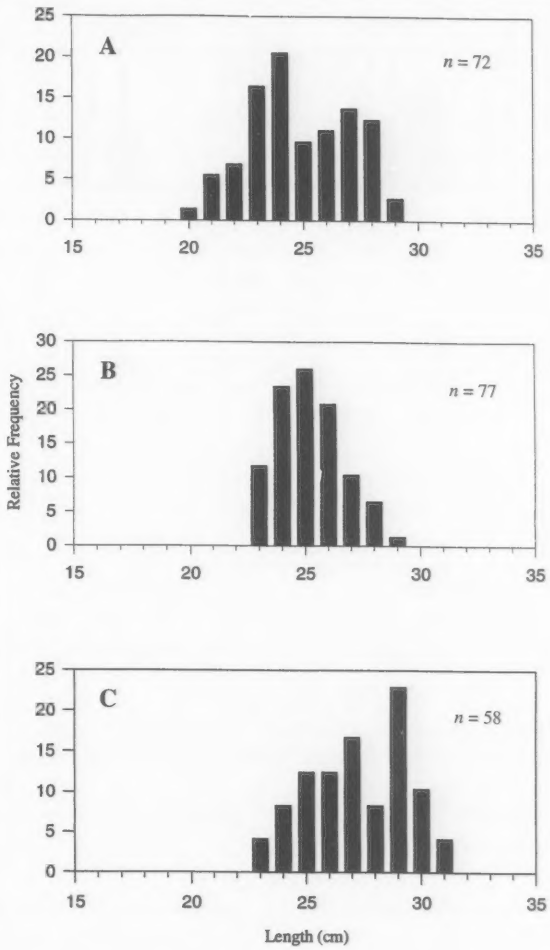


Figure 3

Length-frequency distributions of the (**A**) 1980 spring-hatched, (**B**) 1982 spring-hatched, and (**C**) 1986 autumn-hatched cohorts as immature 3-year-olds in 1983, 1985, and 1989, respectively.

Table 2

Mean lengths and standard deviations of immature western Newfoundland herring from the 1980 and 1982 spring-hatched cohorts as 2- and 3-year-olds in the spring (April–June) and the fall (October–December) fisheries.

1980 spring-hatched cohort						1982 spring-hatched cohort					
Year	Age	Fishery	Mean length (cm)	SD	*n*	Year	Age	Fishery	Mean length (mm)	SD	*n*
1982	2	Spring	—	—	—	1984	2	Spring	187.96	12.87	11
		Fall	248.91	27.23	35			Fall	248.47	15.17	75
1983	3	Spring	247.86	20.87	72	1985	3	Spring	252.11	14.50	77
		Fall	278.80	17.43	585			Fall	283.27	10.56	310

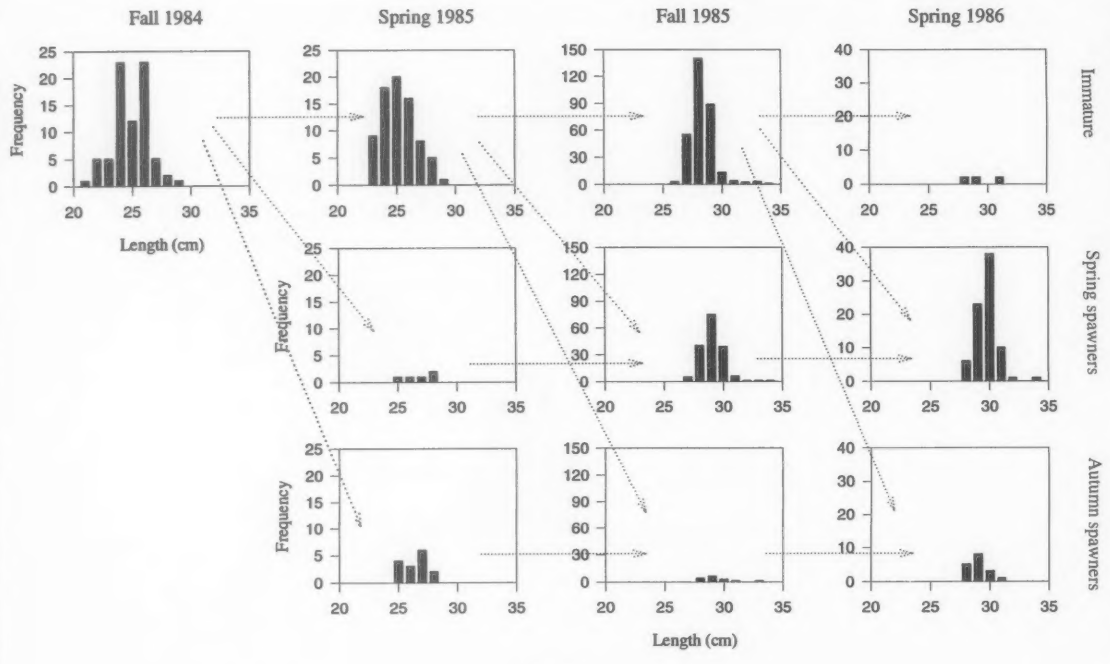


Figure 4

Length-frequency distributions of the 1982 spring-hatched cohort from the fall of 1984 to the spring of 1986, showing the relative proportions of immature herring that eventually adopted either the spring- or the autumn-spawning season as determined by their maturity stages.

same pattern is evident for the 1986 autumn-hatched cohort, which also showed a large bimodal length-frequency distribution at age 3 (Fig. 3C).

The significance of these differences in length composition is shown by following these cohorts as they became mature and began to spawn. We observed that when the length-frequency distribution of the juvenile spring-hatched herring was unimodal and had a relatively small variance (1982 cohort), the majority of them spawned in the spring of 1986 at age 4 (Fig. 4). Conversely, when the juvenile length-frequency distribution was bimodal and had a relatively large variance (1980 cohort), there was an almost even split between those that became spring spawners and those that eventually became autumn spawners (Fig. 5). In addition, if one follows the 1980 spring-hatched cohort after maturity, those that became spring spawners were significantly smaller (*t*-test: $P<0.0001$, SAS Institute Inc., 1985) than those that became autumn spawners (Fig. 6A). This length difference was sustained throughout their early adult life, i.e. from age 3 through age 6. A similar pattern was also seen with the 1979 autumn-hatched cohort. Those that became spring-spawners were smaller at age (Fig. 6B), although the differences are not significant for certain ages owing to small sample sizes.

Discussion

Einarsson (1952) hypothesized that year-class parallelism (twinning) in sympatric seasonal-spawning herring populations came about through a correlation between larval survival conditions in the fall of one year with conditions in the spring of the following year, assuming the larval stage to be the critical phase that determines year-class strength. However, given the ontogeny of the larvae of sympatric seasonal-spawning populations, it is difficult to conceive of a single mechanism by which both cohorts would experience similar survival conditions over a 10-month period, especially since twinning does not normally occur with two successive year classes within the same year. If one follows the development

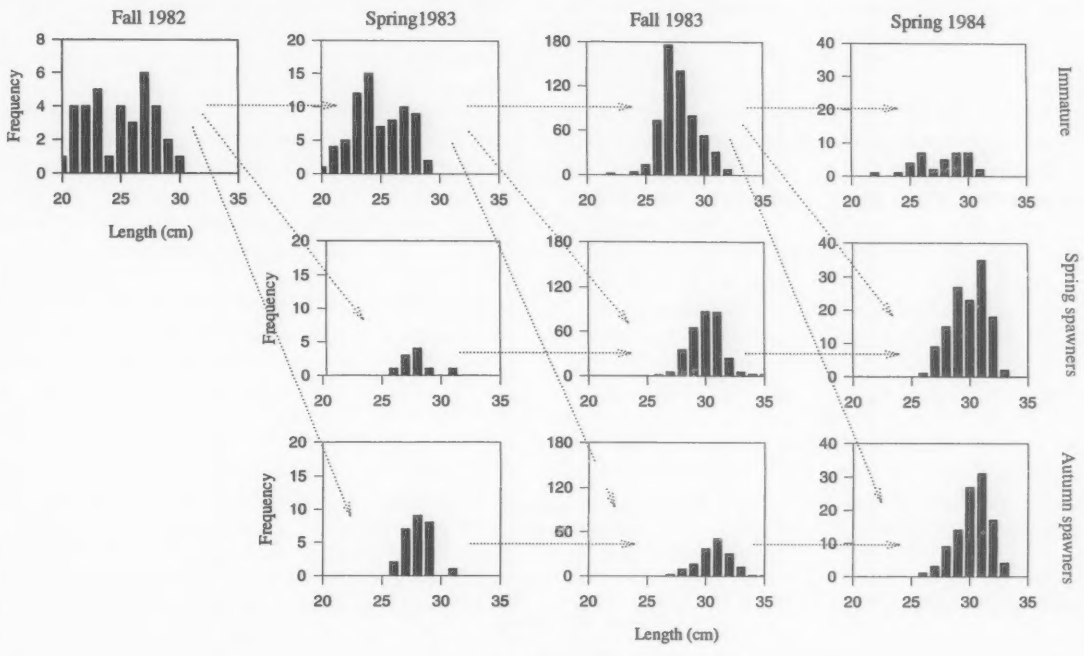


Figure 5

Length-frequency distributions of the 1980 spring-hatched cohort from the fall of 1982 to the spring of 1984, showing the relative proportions of immature herring that eventually adopted either the spring- or the autumn-spawning season as determined by their maturity stages.

of an autumn-hatched cohort and that of the spring-hatched cohort of the following year, from hatching through metamorphosis (Fig. 1), it is apparent that at no time are these two cohorts in the larval stage at the same time, i.e. the autumn spawners have metamorphosed before the spring spawners of the following year have hatched. Autumn-spawned herring in the northwest Atlantic hatch from August to November, remain as larvae throughout the winter (Iles and Sinclair, 1982), and metamorphose within a "window" between March and May (Sinclair and Tremblay, 1984). Larvae hatched in June or July from the spring-spawning event reach the required size for metamorphosis during September or October of their first year. Conditions affecting larval survival would therefore have to be favorable from September of one year to June of the next, but unfavorable between July and August for Einarsson's explanation to be credible.

Einarsson (1952) speculated that a strong standing stock of copepods in the autumn of one year may be correlated with enhanced copepod egg production the following spring, thus favoring larval herring survival over this extended period, although the data available to him did not show this correlation. In addition, these enhanced survival conditions would not only have to exist over a long, but nonetheless precise period of time (September–June), but would also have to be extremely widespread. Twinning occurs in most if not all sympatric herring populations in the northwest Atlantic (de Lafontaine et al., 1991) and sympatric spring- and autumn-spawners do not necessarily use the same breeding locations nor the same larval retention mechanisms, i.e. spring and autumn spawners along the west coast of Newfoundland (McQuinn and Lefebvre[4]).

The present study supports the alternative hypothesis that the twinning of year classes can be explained by the crossover or straying of a significant number of individuals from one seasonal-spawning population to the other. Our results also support the hypothesis of Jean[5], Graham (1962) and Winters et al. (1986) that variable growth rates in the juvenile phase lead to this crossover. Results from several

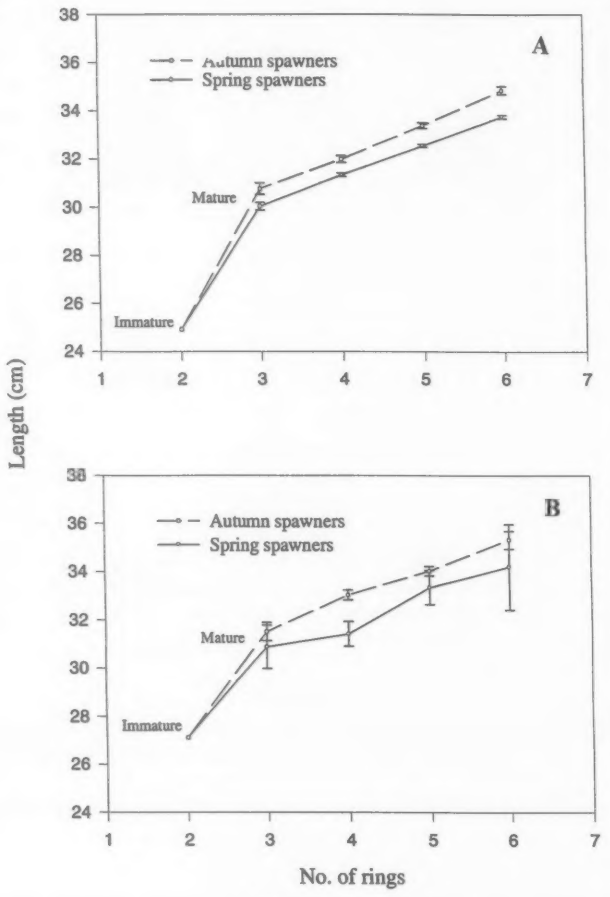


Figure 6

Length at age and 95% CI of the (**A**) 1980 spring-hatched and (**B**) 1979 autumn-hatched cohorts in the late fall (October–December), once the spawning season had been established as determined by their maturity stages for each cohort (age is expressed as the number of otolith rings—see text).

studies have concluded that either density-dependent (Anthony, 1971; Lett and Kohler, 1976) or density-independent factors (Moores and Winter, 1982), or both (Anthony and Fogarty, 1985; Haist and Stocker, 1985), contribute to the significant inter- and intra-annual variations in the growth rates of juvenile herring. There has developed a general consensus among these authors that differences observed in length at age between year classes of adult herring originated in the juvenile phase, before maturation. Further, Toresen (1990) compared the growth of juvenile Norwegian herring from the 1950's with that from the 1970's and concluded that variable growth rates depended mainly on where the juveniles spent their early years. Large cohorts showed both density-dependent growth when these cohorts were distributed in the fjords, as well as environmentally induced growth variations when components of the cohort were distributed in less productive areas of the Barents Sea. This study demonstrated that different components of a single cohort can encounter different growth conditions before maturation and thus can experience different growth rates.

Density-dependent and environmentally induced variability in growth and condition in the juvenile phase is believed to affect the onset of first matura-

tion in several teleost species (Lett and Doubleday, 1976; Holdway and Beamish, 1985; Rowe and Thorpe, 1990), including Atlantic herring (Marti, 1959; Raitt, 1961; Anthony and Fogarty, 1985; Haist and Stocker, 1985). Several studies have concluded that length, rather than age, is the "critical" factor determining the onset of first maturation in herring (Burd, 1962; Beverton, 1963; Toreson; 1990). Variations in growth rates within a cohort, whether they are density-dependent or not, will therefore influence the age at which different components of a cohort will reach the critical length.

We have seen in the present study that variable juvenile growth rates do influence the onset of first maturation in herring (the age of maturity) and thus affect which season is adopted for spawning. When the growth characteristics of a cohort were relatively uniform in early life, as represented by the unimodal length distribution of the immature 1982 cohort as 3-year-olds, most of the cohort subsequently matured in synchrony and spawned in the spring of 1986 as 4-year-olds. However, when the immature 3-year-old length-frequency distribution showed signs of differential growth rates, as with the 1980 spring-hatched and 1986 autumn-hatched cohorts, maturation was asynchronous. Those individuals from the 1980 cohort with an advanced length at age matured as autumn spawners in the fall of 1983 at age 3 years and 4 months. A large proportion of this cohort subsequently spawned the following spring at age 4, and the remainder took advantage of an additional growth season before spawning in the fall of 1984 as autumn spawners. The autumn-spawning individuals of this cohort were therefore significantly longer at age than those of the same cohort that remained spring-spawning (Fig. 6A). Winter et al. (1986) also concluded that the faster-growing spring-hatched individuals matured as autumn-spawners. Conversely, the 1979 autumn-hatched individuals that became spring spawners did so the previous spring at age 3 years and 8 months and thus showed a shorter length at age than those that remained autumn spawners and matured at age 4 (Fig. 6B). We also observed that the adopted season was maintained after the initial spawning because this length difference persisted until at least age 6.

This crossover also explains the observed pattern of twinning—that is to say a strong spring-spawning year class matched with a strong autumn-spawning year class from the previous year. The fact that twinning is seldom seen between spring- and autumn-spawning year classes of the same year is due to the ageing convention for herring (Hunt et al.[8]), which does not consider the possibility of crossover between these populations. The present study has demonstrated that this crossover can occur in both directions, i.e. spring-hatched herring can contribute to a autumn-spawning year class (1980) and vice versa (1986). It should also be mentioned that although the effects of crossover between sympatric herring populations is more striking when large year classes are involved, resulting in year-class twinning, the significant correlation found between subsequent autumn- and spring-spawning year classes in eastern Newfoundland (Winters et al., 1986) indicates that crossover undoubtedly occurs to some extent with all year classes.

The present study therefore does not support the concept of discrete sympatric seasonal-spawning populations in Atlantic herring. The data presented here suggest that the progeny of a given seasonal population do not necessarily recruit to the parental population but may indeed contribute to a local population of another reproductive season. Furthermore, the spawning season that is established at the time of first maturation is maintained for the remainder of adult life.

Acknowledgments

I wish to acknowledge the efforts of Céline Trudeau-Simard and Joanne Hamel for the analysis of the biological samples, including age and hatching-season determinations. I also thank Yvan Lambert and two anonymous reviewers for their helpful comments on the manuscript.

Literature cited

Aneer, G.
1985. Some speculations about the Baltic herring *Clupea harengus membras* in connection with the eutrophication of the Baltic Sea. Can. J. Fish. Aquat. Sci. 42 (suppl. 1):83–90.

Anthony, V. C.
1971. The density dependence of growth of the Atlantic herring in Maine. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 160:197–205.

Anthony, V. C., and M. J. Fogarty.
1985. Environmental effects on recruitment, growth, and vulnerability of Atlantic herring *Clupea harengus harengus* in the Gulf of Maine region. Can. J. Fish. Aquat. Sci. 42 (suppl. 1):158–173.

Baxter, I. G.
1959. Fecundities of winter-spring and summer-autumn herring spawners. J. Cons. Int. Explor. Mer 25(1):73–80.

Beverton, R. J. H.
1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 154:44–67.

Burd, A. C.
1962. Growth and recruitment in the herring of the southern North Sea. Fish. Invest., ser. 2, 23(5), 42 p.

de Lafontaine, Y., S. Demers, and J. Runge.
1991. Pelagic food web interactions and productivity in the Gulf of St. Lawrence: a perspective. *In* J.-C. Therriault (ed.), The Gulf of St. Lawrence: small ocean or big estuary?, p. 99–123. Can. Spec. Publ. Fish. Aquat. Sci. 113.

Einarsson, H.
1951. Racial analyses of Icelandic herrings by means of the otoliths. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 128: 55–74.
1952. On parallelism in the year-class strength of seasonal races of Icelandic herring and its significance. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 131:63–70.

Graham, T. R.
1962. A relationship between growth, hatching and spawning season in Canadian Atlantic herring *Clupea harengus* L. J. Fish. Res. Board Can. 19(5):985–987.

Grant, W. S.
1984. Biochemical population genetics of Atlantic herring *Clupea harengus*. Copeia 1984(2):357–364.

Haegele, C. W., and J. F. Schweigert.
1985. Distribution and characteristics of herring spawning grounds and description of spawning behavior. Can. J. Fish. Aquat. Sci. 42(suppl. 1):39–55.

Haist, V., and M. Stocker.
1985. Growth and maturation of Pacific herring *Clupea harengus pallasi* in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 42(suppl. 1):138–146.

Holdway, D. A., and F. W. H. Beamish.
1985. The effect of growth rate, size and season on oocyte development and maturity of Atlantic cod *Gadus morhua* L. J. Exp. Mar. Biol. Ecol. 85:3–19.

Hourston, A. S.
1982. Homing by Canada's west coast herring to management units and divisions as indicated by tag recoveries. Can. J. Fish. Aquat. Sci. 39:1414–1422.

Iles, T. D., and M. Sinclair.
1982. Atlantic herring: stock discreteness and abundance. Science (Wash., D.C.) 215:627–633.

Jakobsson, J., H. Vilhjálmsson, and S. A. Schopka.
1969. On the biology of the Icelandic herring stocks. Rit Fiskideildar 4(6):1–16.

Kornfield, I., and S. M. Bogdanowicz.
1987. Differentiation of mitochondrial DNA in Atlantic herring, *Clupea harengus*. Fish. Bull. 85(3):561–568.

Lett, P. F., and W. G. Doubleday.
1976. The influence of fluctuations in recruitment on fisheries management strategy, with special reference to southern Gulf of St. Lawrence cod. ICNAF Sel. Pap. 1:171–193.

Lett, P. F., and A. C. Kohler.
1976. Recruitment: a problem of multispecies interaction and environmental perturbations, with special reference to Gulf of St. Lawrence Atlantic herring *Clupea harengus harengus*. J. Fish. Res. Board Can. 33:1353–1371.

Marti, Yu.Yu.
1959. The fundamental stages of the life cycle of Atlantic-Scandinavian herring. Fish. Res. Board Can. Trans. Ser. 167:5–68a.

McQuinn, I. H.
1989. Identification of spring- and autumn-spawning herring (*Clupea harengus harengus*) using maturity stages assigned from a gonadosomatic index model. Can. J. Fish. Aquat. Sci. 46(6):969–980.

Messieh, S. N.
1972. Use of otoliths in identifying herring stocks in the southern Gulf of St. Lawrence and adjacent waters. J. Fish. Res. Board Can. 29:1113–1118.
1976. Fecundity studies on Atlantic herring from the southern Gulf of St. Lawrence and along the Nova Scotia coast. Trans. Amer. Fish. Soc. 105(6): 384–394.

Moores, J. A., and G. H. Winters.
1982. Growth patterns in a Newfoundland Atlantic herring *Clupea harengus harengus* stock. Can. J. Fish. Aquat. Sci. 39:454–461.

Parsons, L. S.
1973. Meristic characteristics of Atlantic herring, *Clupea harengus harengus* L., stocks in Newfoundland and adjacent waters. ICNAF Res. Bull. 10:37–52.

Postuma, K. H.
1974. The nucleus of the herring otolith as a racial character. J. Cons. Int. Explor. Mer 35(2):121–129.

Postuma, K. H., and J. J. Zijlstra.
1958. On the distinction of herring races in the autumn- and winter-spawning herring of the North Sea and English Channel by means of the otoliths and an application of this method in tracing the offspring of the races along the continental coast of the North Sea. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 143(22):130–133.

Raitt, D. F. S.
1961. Otolith studies of southern North Sea herring. J. Cons. Int. Explor. Mer 26:312–328.

Rosenberg, R., and L.-E. Palmen.
1982. Composition of herring stocks in the Skagerrak-Kattegat and the relations of these stocks with those of the North Sea and adjacent waters. Fish. Res. 1:93–104.

Rowe, D. K., and J. E. Thorpe.
1990. Differences in growth between maturing and non-maturing male Atlantic salmon, *Salmo salar* L. parr. J. Fish Biol. 36: 643–658.

Safford, S. E., and H. Booke.
1992. Lack of biochemical genetic and morphometric evidence for discrete stocks of northwest Atlantic herring *Clupea harengus harengus*. Fish. Bull. 90(1):203–210.

SAS Institute, Inc.
1985. SAS user's guide: statistics, version 5 edition. Cary, N.C.: SAS Institute Inc., 956 p.

Sinclair, M., and M. J. Tremblay.
1984. Timing of spawning of Atlantic herring *Clupea harengus harengus* populations and the match-mismatch theory. Can. J. Fish. Aquat. Sci. 41:1055–1065.

Smith, P. J., and A. Jamieson.
1986. Stock discreteness in herrings: a conceptual revolution. Fish. Res. 4:223–234.

Toresen, R.
1990. Long-term changes in growth of Norwegian spring-spawning herring. J. Cons. Int. Explor. Mer 47:48–56.

Wheeler, J. P., and G. H. Winters.
1984a. Homing of Atlantic herring (*Clupea harengus harengus*) in Newfoundland waters as indicated by tagging data. Can. J. Fish. Aquat. Sci. 41:108–117.
1984b. Migrations and stock relationships of east and southeast Newfoundland herring *Clupea harengus*, as shown by tagging studies. J. Northwest Atl. Fish. Sci. 5(2):121–129.

Winters, G. H., J. P. Wheeler, and E. L. Dalley.
1986. Survival of a herring stock subjected to a catastrophic event and fluctuating environmental conditions. J. Cons. Int. Explor. Mer 43: 26–42.

Nursery habitat in relation to production of juvenile pink snapper, *Pristipomoides filamentosus*, in the Hawaiian Archipelago

Frank A. Parrish
Edward E. DeMartini
Denise M. Ellis

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96822-2396

E-mail address: Frank.Parrish@noaa.gov

Abstract.-Densities of juveniles of the Hawaiian deepwater snapper *Pristipomoides filamentosus* were surveyed for 3 years in relation to their demersal environment at an east Oahu study site. Juveniles settled annually to spatially stable aggregations, occupying expanses of uniform sedimentary habitat. Habitat data were collected and used in a logistic regression model to predict correctly 68% of the juveniles' spatial variability. Premium habitat was identified as a sediment bottom, free of relief, and close to focused sources of drainage (reef platforms, embayments, and anthropogenic sources) in adjacent shallows. Surveys for juveniles elsewhere on insular slopes of the Hawaiian Archipelago indicated low juvenile abundance except at infrequent locations close to point sources of coastal drainage. Estimates of recruit production, based on densities of juveniles from other than premium habitat, were a small fraction of the recruits needed (calculated from catch) to account for the fishery's current landings of adult snappers. The 68-fold higher juvenile abundance at premium habitat can reconcile this difference, indicating that such infrequent high-quality habitat is an important (perhaps critical) fishery resource.

Manuscript accepted 17 July 1996.
Fishery Bulletin 95:137–148 (1997).

Understanding favorable nursery habitat and its contribution to the standing stock of adults provides an important perspective for managing demersal fisheries. In the tropics, such nursery habitat has been studied effectively for many species inhabiting shallower depths (Bardach, 1959; Parrish, 1989; Birkeland [1]). Species using deeper, more remote nursery grounds have received less attention, and as a result, habitat often is not considered adequately in fishery modelling or management planning. In places with limited demersal nursery habitat, such as the minimal shelf area of oceanic islands, this habitat may represent a resource of critical importance to the fishery. Accelerated coastal development on many islands could degrade unrecognized favorable nursery habitat and impact fishery resources. This paper examines the nursery habitat of the deepwater Hawaiian pink snapper, *Pristipomoides filamentosus*, in relation to the spatial variability of its juveniles. A study site at a productive nursery ground was intensively surveyed, and the results compared with surveys made over much of the archipelago. The implications of the variable habitat quality for the stock of adult snappers inhabiting the archipelago were then considered.

The pink snapper accounts for more than 40% of the State of Hawaii's $3 million annual commercial bottomfish catch [2] and is well represented in the extensive recreational catch. However, study and management of the adult stock has been historically difficult because of its patchy distribution and poorly recorded recreational landings (Ralston and Polovina, 1982). A productive research approach may be to study the juveniles of the species, which are free of fishing pressure and of the factors that affect recruitment to the adult population. Recent discovery (F. A. Parrish, 1989) of a dense, stable aggregation of juveniles in a nursery area has made this approach feasible. Juveniles (7–25 cm fork length [FL]) occupy moderate depths (60–90 m) in patchy aggregations on the insular shelf for less than a year before moving deeper (150–190 m) as they mature

[1] Birkeland, C. 1985. Ecological interactions between mangroves, seagrass beds, and coral reefs. United Nations Environmental Program Regional Series Report and Studies 73, 126 p.

[2] WPRFMC (Western Pacific Regional Fishery Management Council). 1993. Bottomfish and seamount groundfish fisheries of the Western Pacific region. NOAA NA17FC0062-02, Honolulu, HI, 57 p. WPRFMC, 1164 Bishop Street, Suite 1405, Honolulu, HI 96813.

(Moffitt and Parrish, 1996). Sonic tracks of these juveniles indicate a discrete and limited individual home range of 140 m average diameter, suggesting that the locations of these juvenile aggregations could be very stable. Why juvenile aggregations appear spatially stable and how common they are in the rest of the archipelago are the primary focus of this work.

Methods

Survey of the east Oahu study site

The east Oahu study site contains three submarine canyons. Two of the canyons are located just outside Kaneohe Bay, north of Mokapu Point, and the third is located south of Mokapu Point just outside Kailua Bay (Fig. 1, II). Throughout this paper, the three areas will be referred to as the "north Kaneohe," "south Kaneohe," and "Kailua" canyons. Positional data from a Global Positioning System (GPS) were entered and manipulated in a raster-based Geographic Information System (GIS)(IDRISI 4.0 version) (Eastman, 1992).

Video index of snapper abundance

A baited video camera (Fig. 2) was selected as the primary gear because it provided information on the abundance of snappers and their associated habitat type. In each video drop, the baited camera was placed on the bottom for 10 minutes, where it attracted juvenile snappers in front of the camera lens; the maximum number of snappers seen in a single image was used as the index of abundance. Consecutively deployed video drops were separated by 1,200 m to avoid attraction of fish from previous drops. A description of equipment, method, and validation of the technique for creating a video index of snapper abundance is provided by Ellis and DeMartini (1995).

Selected video stations at the study site were replicated to determine the suitability of unreplicated spatial data for subsequent use in evaluating the persistence of snapper patches over time. Nineteen stations, resampled after 10 days, were used to represent all 3 canyons during February–March 1994. These stations were termed "multicanyon stations."

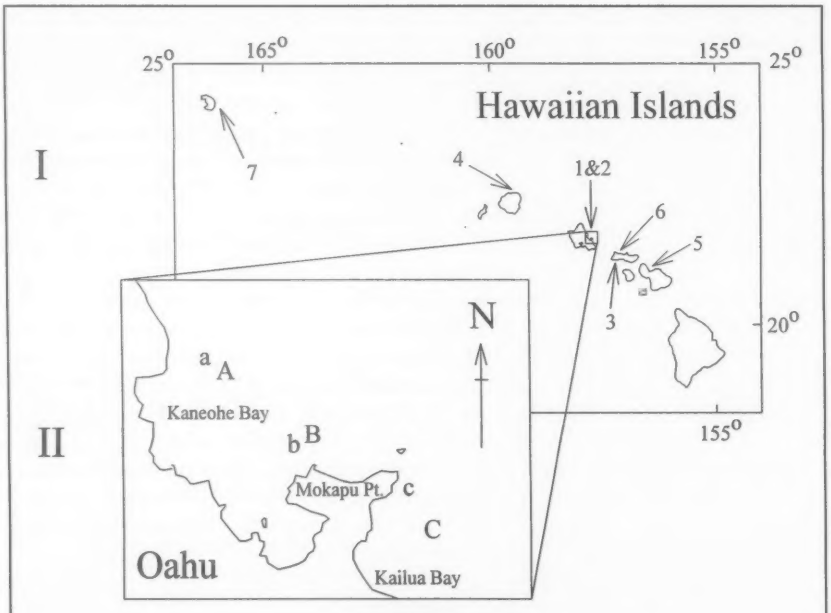


Figure 1

(I) - Map of the Hawaiian Archipelago with video survey sites denoted as 1 = Kailua-Oahu, 2 = Kaneohe-Oahu, 3 = south Molokai, 4 = Hanalei-Kauai, 5 = Kahului-Maui, 6 = north Molokai, and 7 = French Frigate Shoals in the Northwestern Hawaiian Islands. (II) Locations of the three east Oahu areas studied, including north Kaneohe canyon (A), south Kaneohe canyon (B), and Kailua canyon (C). Also represented are the sources of coastal drainage of north Kaneohe channel (a), south Kaneohe channel (b), and the Kailua wastewater outfall (c).

Interannual fidelity of snapper recruitment to the study site was assessed by using 20 video stations in the north Kaneohe canyon during 4 surveys in May 1992, May 1993, September 1993, and June 1994. These were designated as "multiyear stations" and were compared by using date of survey as a covariate.

Habitat characteristics

Slope, substrate type, sediment particle size, and proximity to closest known point sources of focused coastal drainage (channels through reefs and wastewater outfalls) were determined for all areas. The effect of slope on snapper abundance was assessed by using a GIS slope algorithm with collected bathymetry data. At the depths frequented by juvenile snappers, the habitat is typically dominated by a featureless expanse of sediment. To test the effect of alternative substrates on snapper abundance, types of substrate (as identified in video and chromoscope images) were coded as categories: e.g. soft sediments, escarpment-type relief (exposed edges of shelf, about 3 m high), and hard, even bottom. Video drops that recorded alternate substrate, or were within a snapper home range (Moffitt and Parrish, 1996) of such observations, were compared with video drops on soft sediment, presumably away from the influence of the other substrate. Substrate of adjacent shallower (30–60 m) and deeper (90–120 m) habitats, where juveniles have been historically absent (F.A. Parrish, 1989; Moffitt and Parrish, 1996), were surveyed with a longshore transect of 14 video drops in each of the 2 depth ranges.

Ten bottom grab transects perpendicular to the bottom contours, each sampling 3 depths (45, 76, 106 m), were used to assess a possible relationship between snapper abundance and particle sizes in the sedimentary habitat. Replicate grabs were taken in line with and between the axes of the canyons in each area. Samples were wet-sieved into five size categories (>2.0, 0.35–2.0, 0.149–0.35, 0.0625–0.149, and <0.0625 mm).

The effect of some notable sources of natural and anthropogenic drainage present in each of the three canyons was considered. In Kaneohe, bay water drains through narrow channels (one in the north and one in the south, each with maximum depth of ~15 m at the seaward end) in the reef during ebb tide[3] (Fig. 1, II). In Kailua, increased suspended materials are introduced from an island wastewater and sewage outfall.[4] The video index of snapper abun-

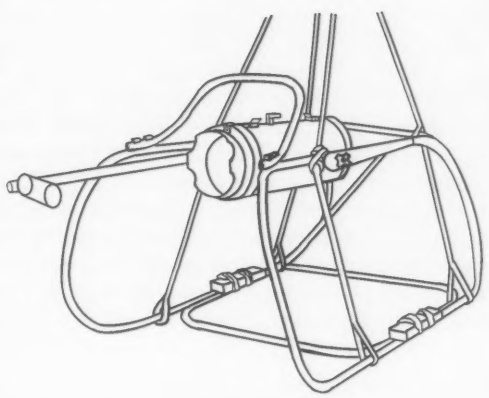


Figure 2

Diagram of the video camera system complete with bait canister mounted 60 cm in front of the lens. Source: Ellis and DeMartini (1995).

[3] Bathen, K. H. 1968. A descriptive study of the physical oceanography of Kaneohe Bay. Oahu, Hawaii. HIMB Tech. Rep. 14, 353 p. Univ. Hawaii, 2550 The Mall, Honolulu, HI 96822.

[4] City and County of Honolulu. 1993–1994. Discharge monitoring reports. Environmental Protection Agency form 3320-1. Wastewater Division, 650 South King St. Honolulu, HI 96813.

Table 1

Depth, mean daily volume, and suspended load of the east Oahu drainage sources. The Kaneohe channels provide tidal drainage; the Kailua discharge is anthropogenic (24 hours).

Source of discharge	Discharge volume (m^3/day)	Discharge depth (m)	Suspended solids (kg/day)	Source
North Kaneohe channel	18.5×10^6	0–15	—	Bathen[1]
South Kaneohe channel	12.9×10^6	0–15	—	Bathen[1]
Kailua wastewater outfall	41,000	30	1,000	City and County of Honolulu[2]

[1]See Footnote 3 in the main body of the text.
[2]See Footnote 4 in the main body of the text.

dance was compared with the volume of each source's discharge (Table 1) divided by the distance separating the video samples from the nearest source of discharge. No attempt was made to sample the nutrients or suspended materials of these discharges. Elevated organics associated with these water masses are documented in the literature (Bromwell, 1992; City and County of Honolulu[4]; Laws and Allen[5]).

East Oahu statistical analysis

The distribution of the data and the categorical nature of the habitat variables required the use of nonparametric analysis (Siegel and Castellan, 1988). The type-I error for statistical significance was set at 0.05 (2-tailed test). Kruskal-Wallis ANOVA (K-W) was used to assess station effects in both "multicanyon and multiyear" analyses and to assess the effect of substrate type.

Differences in substrate by depth were tested with chi-square analysis. Replicate bottom grabs were compared by using Wilcoxon matched pairs sign ranks (MPSR), and Spearman's correlation was used for association of snappers with slope, sediment fractions, and influence of drainage.

Spatial variation of ranked snapper abundance was related to all habitat variables together by using logistic regression. Snapper abundance was grouped into two categories, aggregation present ($n \geq 5$) and aggregation absent ($n < 5$), and assessed relative to the habitat variables that significantly influenced snapper abundance in the previously described univariate analyses (Norusis, 1992). Models of the variables and their plausible interaction effects were explored with the simple logistic regression model (Kleinbaum, 1992):

$$\pi = \frac{e^{\sum B_i X_i}}{1 + e^{\sum B_i X_i}}, \qquad (1)$$

where π is the probability of detecting snappers with the linear combination of the habitat variables X_i in a given location. The coefficients estimated with the nonlinear regression by using maximum likelihood are represented by B_i. The base of the natural logarithm is e. The P-value for retention of independent variables in the model was set at 0.01.

[5] Laws, E. A., and C. B. Allen. 1993. Impact of land runoff on water quality in Kaneohe Bay, a subtropical Hawaiian estuary. Proceedings of the first biennial symposium for main Hawaiian islands marine resources investigation, November 17–18. Hawaii Department of Land and Natural Resource Technical Report 95-01, p. 232–248. Hawaii Dep. Land Natl. Resources, 1151 Punchbowl, Honolulu, HI 96813.

Survey of the archipelago

Conventional fishing gear (e.g. trawls, longlines, traps, handlines) was used to survey a total of 332 km of longshore habitat dispersed over seven islands of the archipelago (1989–94). The effectiveness of each gear at catching juvenile snappers was tested at the east Oahu study site. Sites surveyed included areas outside of embayments, places with large shelf areas at snapper depths, and sites of previous research fishing where juveniles had been documented incidentally (Struhsaker, 1973). Sites where snappers were found were then reassessed with longshore baited video surveys (range 5.5–42.6 km) to permit comparison with snapper abundance at the east Oahu study site. Numbers of juvenile snappers observed at each site were standardized by effort. The distance of each video drop from the coastal reef edge (15-m isobath) and the type of substrate seen in the video image were tabulated for each site; these variables were then compared with the respective video index of juvenile snapper abundance. Catch-per-unit-of-effort (CPUE) data from sets of conventional fishing gear at these coastlines were included to provide an independent index of snapper abundance.

In comparing video data from other coastlines with those of east Oahu, data for the two Kaneohe areas were pooled. Coastlines with point sources of drainage were identified, and the distance between sources of discharge and the video drops (weighted for maximum depth of discharge) were calculated. Importance of proximity to drainage sources to snapper abundance was then evaluated for these archipelago sites.

Snapper production estimates

To assess the importance of the contribution of juveniles from a site with premium habitat (e.g. Kaneohe) to the adult fishery, the adequacy of recruit production from other habitat areas was estimated. The density of snappers at habitat without snapper aggregations was compared with the density of snappers needed to explain the catch from the main Hawaiian Islands (MHI) commercial snapper fishery. Derived from mandatory reporting from the commercial fishery, the estimate is based on the catch of ~3-year-old snappers (termed "immature") just entering the MHI adult snapper fishery (Ralston, 1981; DeMartini et al., 1994). Based on the years 1989–92, the estimated mean annual catch, C (i.e. the commercial catch [WPRFMC[2]]) was ~22,000 immature (1.3 kg) snapper/year. Recreational fishing produces a significant additional catch in Hawaii, but it is poorly documented and was not considered in this estimate.

By using the estimated growth coefficient, k, of 0.25/yr derived for juvenile snappers (DeMartini et al., 1994) in the mortality relationship of $M/k \approx 2$ (Ralston, 1987a), the instantaneous natural mortality coefficient, M, was estimated as 0.50/yr, and a range for the instantaneous fishing mortality coefficient, F, was calculated. The low end of the range assumes $M = F$, on the basis of the fishery operating at maximum sustainable yield (Ralston and Polovina, 1982), providing an instantaneous F of 0.50/yr. The high end of the range assumes that fishing mortality is twice natural mortality, $F = 2M$ (Ralston, 1987b), resulting in an F of 1.0/yr. The two estimates of F were used independently to represent the extremes of the probable range. The mean standing stock of immature snappers, N_3, can be calculated by use of the conventional formula for the annual rate of exploitation (Everhart and Youngs, 1981; Gulland, 1983):

$$N_3 = \frac{C}{\frac{F}{F+M}\left(1-e^{-[F+M]}\right)}, \qquad (2)$$

resulting in estimates of 42,500–69,600 fish. Because these immature snappers have been exposed to natural mortality for 2 years since the time t_1 that they inhabited nursery depths, a back calculation provides N_1, an initial estimate of juveniles supported on the MHI grounds. The formula (Gulland, 1983)

$$N_1 = \frac{N_3}{e^{-M(t_3-t_1)}}, \qquad (3)$$

yielded values of N_1 between 115,600 and 189,200 fish. With this estimate of N_1, divided by the amount of bottom area in the MHI between the 60 and 90 m isobaths (2,600 km^2, NOS bathymetric charts), an estimate of the overall density of juvenile snappers required to support the current fishery was derived.

Results

The east Oahu study site

Two-hundred and eleven video camera drops with standard bait were dispersed throughout the insular slope (60–90 m depth) of the Oahu study site. Abundance data from the video drops were nonnormally distributed (33% zero observations) (Fig. 3). Snappers were found at each of the 3 east Oahu canyons. Snapper abundance differed significantly among the multicanyon stations (K-W, χ^2=35.6, P<0.01), confirming that relative spatial differences in snapper distribution remain stable (Fig. 4). In the multiyear stations at north Kaneohe canyon, essentially similar spatial differences persisted (K-W, χ^2=37.3, P<0.01); this finding suggests that successive years of juvenile snappers settle spatially according to habitat quality. Because the effect of station was significant for both the multicanyon and multiyear comparisons, the abundances of snappers at unreplicated video drops were considered representative of the habitat quality at those locations.

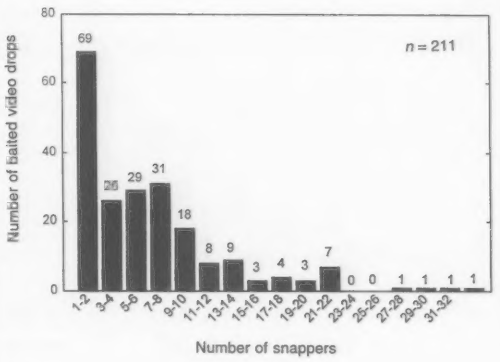


Figure 3

Distribution of occurrence of snappers in video drops at east Oahu sites.

Bottom slope was unrelated to the video indices of snapper abundance (Spearman's r_s=0.013, P=0.72). Substrate at 95% of the video drops (60–90 m) was composed of uniform, smooth sediment. High, escarpment-type relief was detected in only 3% of the drops. A significantly lower abundance of snappers occurred in the area surrounding escarpment-type relief than in the even sediment bottom (χ^2=11.48, P<0.001). The 95% confidence intervals of snapper densities at sites with relief (0–1 snappers) versus sites with sediment bottom (3–4 snappers) did not overlap. A similarly low abundance of snappers was associated with areas near exposed hard substrate (χ^2=10.50, P<0.01; 95% CI=0–2 snappers). Snapper grounds (60–90 m) and the adjacent deeper (90–120 m) area did not differ in the occurrence of soft sediment substrate (χ^2=0.44, P=0.43). However, the adjacent shallow grounds (30–60 m) had significantly more hard bottom and relief (χ^2=11.36, P<0.001); soft sediment occurred in fewer (71%) of the shallow video images.

The duplicate sediment grabs did not differ, suggesting that the sediment sampling effectively represented the soft bottom habitat (Wilcoxon MPSR, P=0.93). Of the 5 sediment fractions, snapper abun-

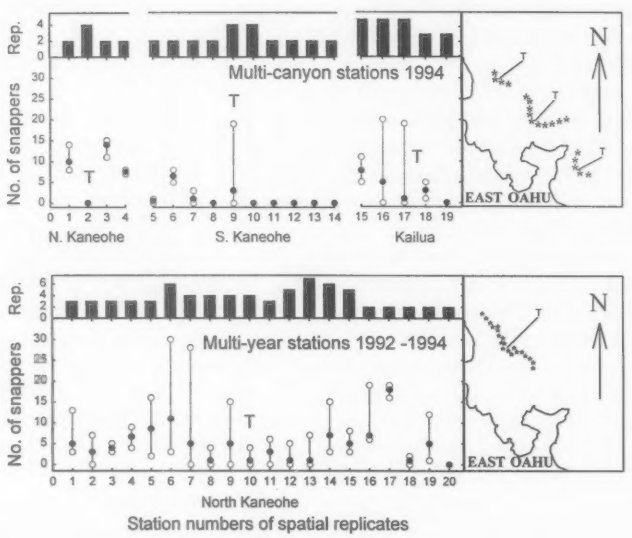


Figure 4

Mean (filled circle) and range (hollow circles) of east Oahu snapper station reliability test. The top graph is the 1994 multicanyon analysis and the bottom graph is the multiyear assessment (1992–94). The "T" on each graph represents the location of each canyon's axis or "trough." Numbers of replicates (Rep.) at each station are represented with bar graphs at the top of each graph. Maps on the right of each graph indicate the areas covered by the data.

dance was significantly correlated with only the clay-silt (<0.0625 mm) fraction (Spearman's r_s=0.35, P<0.001) (Table 2). The greatest abundance of clay-silt occurred in an area just northwest of the north Kaneohe canyon trough; at Kailua the abundance was less than half that at Kaneohe, and high concentrations spread southeast of the canyon trough.

Proximity of point sources of drainage was associated with snapper abundance, i.e. video index of snapper abundance and distance to discharge were significantly negatively correlated (r_s=–0.18, P<0.05). The weakness of the relationship resulted from the failure to consider the effect of bottom relief in the comparison. This result indicated the need for a model that considered the variables together.

Table 2

Spearman rank order correlation coefficients and probability values for snapper abundance with sediment particle size. In all comparisons sample size = 211.

Sediment size fraction (mm)	Correlation coefficient r_s	Probability value P
>2.000	–0.0426	0.54
0.350–2.000	–0.0932	0.178
0.149–0.350	–0.0922	0.184
0.063–0.149	0.0809	0.244
<0.063 (clay-silt)	0.3555	<0.001

Modeling of snapper aggregations.

The stepwise backward regression evaluated the relative importance of the 3 habitat variables found significant in the univariate analysis: 1) escarpment-type relief; 2) clay-silt (<0.0625 mm) sediment fraction; and 3) proximity of coastal discharge. The interaction of discharge with the presence of clay-silt was also assessed. All variables except clay-silt were retained by the model (P<0.01; Table 3). Reasons for the model's exclusion of clay-silt will be discussed later. The model correctly predicted overall presence (≥5) or absence (<5) of snapper aggregations for 68% of the video drops. The model predictions of presence (79% [≥5]) were roughly balanced by those for absence (60% [<5]) (Table 4). Ranked snapper abundance was interpolated by using all video drops to

Table 3

Statistical specifics associated with the regression for presence (≥5) or absence (<5), of snapper aggregations at east Oahu. Model chi-square (χ^2)=54.11, P<0.0001, df=3.

Name of variable	Estimated coefficient	Standard error	Probability value P
Cross product of clay-silt with proximity of drainage source	1.45×10^{-6}	3.47×10^{-7}	<0.0001
Distance to drainage	-7.5×10^{-7}	1.58×10^{-7}	<0.0001
Escarpment relief	−1.586	0.435	0.0003

provide an image of snapper distribution at east Oahu (Fig. 5).

Table 4

Two by two table of presence (≥5) or absence (<5) of snapper aggregations predicted by the model versus presence or absence observed from baited video drops. Includes all 211 drops at east Oahu.

	Predicted by model		
Observed	Aggregations absent (<5)	Aggregations present (≥5)	Percent correct
Aggregation absent	73	48	60
Aggregation present	19	71	79
			68 overall

Abundance of juveniles in the archipelago

Fishing surveys at insular slopes other than east Oahu (total 332 km) detected few juveniles (Table 5). Five of these sites (with snappers) were surveyed with video camera to compare with the east Oahu aggregations. Significant numbers of snappers were found only at a site off the southwest end of the island of Molokai (Sept 1993). A repeat video survey indicated that the significant between-station differences in snapper abundance initially reported at South Molokai, persisted 7 months later (K-W, χ^2=50.8, P<0.05) (Fig. 6).

The video index and CPUE of the conventional fishing gear were roughly consistent for all sites (Table 6). Snapper abundance was found unrelated to substrate type (r_s=0.59, P=0.40, n=7) or distance from the 15-m isobath (r_s=–0.84, P=0.15, n=7). However, distance/depth of discharge at the four sites with known sources of coastal drainage (Kaneohe, Kailua, S. Molokai, and Hanalei) were associated with snapper abundance (r_s=–1.0, P<0.001, n=4).

Video- and catch-based production estimates

Video abundance data from MHI sites at N. Molokai, Hanalei, and Kahului yielded a mean estimated den-

Table 5

Fishing effort, length of slope fished, and total snappers caught on surveys of Hawaiian insular slopes for juvenile snappers.

Island	Bottom trawls 1990 (no.)	Bottom longlines 1992 (no. hooks)	Fish traps 1989–94 (no.)	Handlining 1993–94 (line-hr)	Length of slope fished (km)	Total snapper caught (no.)
Oahu[1]	16 (5)[2]	— (150)	27 (53)	60 (50)	164 (14)	16 (828)
Molokai	26	—	101	87	60	256
Maui	6	150	—	—	16	4
Lanai	6	—	—	—	16	0
Kauai	—	150	—	—	18	3
Necker	—	—	25	—	16	0
FFS[3]	—	—	63	—	42	5
Total	54	300	216	147	332	284

[1] The east Oahu study site values are not included in any of the figured totals.
[2] Numbers in parentheses represent additional values from gear validation test done at the east Oahu site.
[3] FFS = French Frigate Shoals.

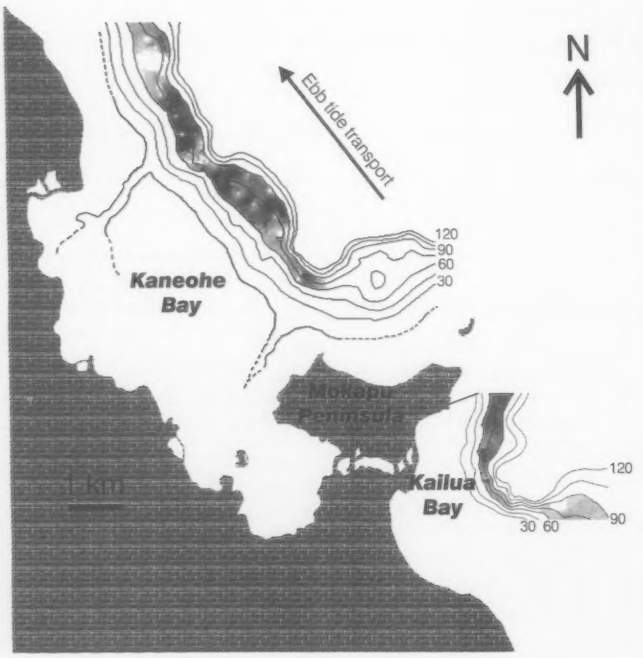


Figure 5

Interpolation of snapper abundance from all video deployments at the east Oahu study site (north Kaneohe, south Kaneohe, and Kailua). Increasing snapper abundance is signified with darker shading. Both north and south channels of Kaneohe Bay are contoured on the map, and a line is used to indicate the eastward extension of the Kailua outfall from the Mokapu pennisula. Isobaths are in 15-m intervals.

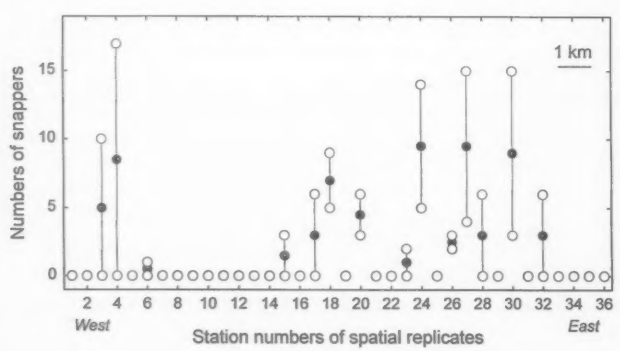


Figure 6

Mean (filled circle) and range (hollow circles) of number of snappers seen per video drop on south Molokai coastline survey. Each station received two video deployments. The drainage from the Kahanui swamp enters the ocean ~1 km to the east of extreme right of the graph.

sity of 6.6 snappers/km^2, which was taken as representative of routine "nonpremium" habitat. Assuming this density and a uniform distribution of snappers at a large scale, we estimated that the 2,600 km^2 of available habitat at 60–90 m depth in the MHI is equivalent to 17,200 juvenile snappers. This video-based estimate is no more than 15% of the 115,600–189,200 juvenile snappers (44–72 snappers/km^2) backcalculated from catch in the commercial fishery. A pilot study of recreational fishing[6] suggests that if recreational catch was included in the back calculation, the difference between video and catch estimates could be as high as one order of magnitude.

Discussion

Premium nursery habitat

Persistence of specific snapper aggregations on east Oahu was supported by both the multicanyon and multiyear analyses. However, because no multiyear surveys extended beyond the north Kaneohe site, we can only assume that year-to-year variability in the other east Oahu sites was similar. A strong year class of snappers might be expected to force some individuals to occupy marginal habitat, making the distinction between snapper aggregations less clear. Results of the multiyear survey indicated that 1993 and 1994 were relatively poor years for recruitment of young snappers, suggesting that the observed snappers in the multicanyon stations occupied favorable habitat.

Slope showed no significant effect on the distribution of snappers, but relief did. The deep sediment deposits on the terraces preclude any undetected small-scale relief features to which juveniles might orient. The few areas where escarpment features protruded from the sediment layer were associated with ab-

[6] Hamm, D. C., and H. K. Lum. 1992. Preliminary results of the Hawaii small-boat fisheries survey. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Sci. Cent. Admin. Rep. H-92-08, 35 p.

sence of snapper aggregations in the logistic model. This finding supports the hypothesis that structural relief or its associated community represents conditions less favorable or more hazardous to the snappers (greater interspecific competition, risk of predation, etc.) (Johannes, 1978; F. A. Parrish, 1989). Expanses of uniform sediment bottom are obviously an important substrate feature. The relative scarcity of this habitat observed at depths <60 m at least partly explains the absence of snappers on the shallower (30–60 m) grounds.

Proximity to point sources of drainage and its relationship with the presence of clay-silt sediment can explain much of the snappers' longshore distribution. Work with first-year juveniles of species of *Pagrus* has demonstrated that substrate and associated water flow are important to habitat selection (Francis, 1995). Improved availability of food has been proposed as a reason for fish demonstrating habitat preferences (Sudo et al., 1983). Distributions of sediment particle sizes such as clay-silt have been shown to enhance the localized distribution of certain benthic invertebrate infauna (Fegley, 1988). A favorable localized sediment composition might contribute to an enhanced forage base for juvenile fish (Tito de Morais and Bodiou, 1984). However, these longshore variations in clay-silt abundance are simply indicative of the longshore differences in coastal water flow that disperse the flocculent clay-silt. The highest fraction of clay-silt is found at the seaward end of the north Kaneohe channel, where snapper abundance is high and bay drainage is most concentrated. The density of fish in Kailua is greatest near the wastewater outfall, where the clay-silt fraction is lowest. The outfall introduces and increases the frequency of drifting materials to the area, similar to the flow of natural drainage sources, but without creating a clay-silt dispersion field. For this reason, the logistic model excluded the variable

Table 6

Characteristics and results of longshore coastal surveys for snappers at 7 sites.

Location (year) and "figure ID number"	Longshore distance surveyed (sampling interval) (km)	Index of abundance			Uniform sediment seen in survey (%)	Mean distance of video drops from 15 m isobath and range (km)	Source of coastal drainage (max. depth of source in meters)
		Video sampling mean no./ video drop	Conventional research fishing (mean no.)				
			Longline set	Trap set			
Kailua, Oahu (1994) "1"	4.6 (1)	24.8	—	—	88	1 (0.61–1.3)	Kailua wastewater outfall (30)
Kaneohe, Oahu (1992–94) "2"	13.8 (0.5)	4.5	3.8	5.78	95	1.24 (0.64–1.6)	Kaneohe Bay, north and south channels (15)
South Molokai (1993–94) "3"	16.6 (0.5)	1.97	—	2.0	81	1.6 (0.87–3.9)	Kahanui swamp and fringing reef drainage (15)
Hanalei, Kauai (1992) "4"	18.5 (1.5)	0.22	0.20	—	52	1.5 (0.77–4.2)	Hanalei estuary
Kahului, Maui (1992) "5"	15.7 (1.5)	0.03	0.01	—	92	4.3 (1.6–10.5)	None known
North Molokai (1994) "6"	5.5 (0.5)	0	—	0.007	92	0.87 (0.64–1.2)	None known
French Frigate Shoals (1993) "7"	42.6 (1.5)	0	—	0.037	40	1.3 (0.92–2.3)	None known

Figure ID numbers listed in first column correspond with survey sites shown in Figure 1, I.

clay-silt. This finding suggests that the distribution of juveniles within the preferred uniform sediment habitat is related more closely to water flow than to sediment particle size. Similar enhanced abundances of fish associated with anthropogenic sources have been proposed elsewhere (Mearns, 1974; Monaco et al., 1992) and in Hawaii (Henderson, 1992; Grigg, 1994).

In video deployments at many study sites, snappers were observed routinely picking at items in the lower water column and mouthing the substrate. DeMartini et al. (1996) determined that juvenile snappers at the north Kaneohe canyon eat a mixture of gelatinous drift, demersal crustaceans (amphipods, etc.), and benthos (micromollusks, annelids, etc.). The majority of prey were <1 cm, of low motility, and bottom associated.

Habitats receiving drainage from shallower environments might have their food supply enhanced in at least two ways. First, fish may encounter and feed more frequently on suspended organisms and other materials flushed from shallower reef and estuarine environments (Gerber and Marshall, 1974). Second, the flow from shallow sources may elevate the organics in sediments, thereby enhancing production of the benthos that snappers eat. Changes in benthic fauna at comparable depths (50–200 m) have been documented in relation to the flux of organics in the water column—both in natural (Buchanan and Moore, 1986) and anthropogenic situations (Nichols, 1985). Benthos may also become enriched during large episodic movements of nutrient-rich bay sediment to localized areas in the snapper grounds. The significant interaction, identified by the logistic model, of clay-silt with proximity to drainage sources supports the notion of enhanced organic input to the benthic community provided by such drainage.

Distribution of juveniles in the archipelago

Conventional fishing on the insular slopes of the archipelago (332 km) identified few sites with juvenile snappers; the mode and median of the catch of juveniles from all the gear was zero. Except for aggregation sites at Oahu and Molokai, catches of juveniles occurred only in token numbers. In a 1967–68 demersal trawl survey (n=62), Struhsaker sampled ~90 km of relevant depths in the main Hawaiian Islands and similarly found the occurrence of juveniles to be infrequent and patchy. His catches of juvenile snappers had a mode of zero and median of one (Struhsaker, 1973).

The 5 sites other than east Oahu that were surveyed by video (Table 6) each had substrate and depths consistent with those at east Oahu; 2 had sources of drainage; but only 1, south Molokai, supported a snapper aggregation. South Molokai's Kahanui swamp, located within the island's extensive fringing reef complex, has a drainage channel similar in width and depth (15 m) to north Kaneohe Bay (U.S. Army Corps of Engineers, 1984). Its associated snapper aggregation is well situated to exploit the tidal drainage of the reef platform and swamp dispersed by westbound currents of the area[7] (Fig. 6). The Hanalei estuary, on the island of Kauai, probably fails to influence snapper depths because it discharges at a zone of high-energy mixing (~1 m depth) too far inshore from juvenile snapper grounds.[8] The site at Kahului, Maui, would have to have a very large coastal drainage feature to aggregate snappers; the distance between the snapper grounds and such a source would be twice that of the other sites surveyed. Presumably, any source of increased suspended materials (embayments, reef platforms, or atoll lagoons) could enhance snapper aggregations if depth, distance, and circulation characteristics focused water and increased the frequency of suspended materials close to juvenile grounds (Cyrus and Blaber, 1983; Birkeland, 1984).

Struhsaker, during his 1967–68 trawl survey, identified one location (north coast of Oahu) with catches as high as 180 individuals in one haul. The substrate at the site was composed of uniform sediment and received discharge from two north Oahu rivers. However, according to the surveys from the present work, the snapper depths at this site seem almost too far offshore (mean=4.5 km) to support an aggregation. Numerous attempts in 1990 (Table 5) to relocate this north Oahu aggregation with the same gear that was used in 1967–68 did not yield any snappers. Many changes that could have modified the suitability of this habitat for juveniles (e.g. heavy exploitation of the snapper stock [WPRFMC[2]]; collapse of the coast's large-scale irrigation-based agriculture and its drainage; effects of increasing relief on juvenile grounds from the accumulation of incidental ocean dumping) have occurred in the 22 years between the surveys.

Implications for the fish stock

Regardless of what factors create premium habitat, the implications for the snapper stock of the archi-

[7] Wyrtki, K., V. Graefe, and W. M. Patzert. 1969. Current observations in the Hawaiian Archipelago. Hawaii Institute of Geophysics HIG-69-15, 27 p. Hawaii Inst. Geophysics, 2525 Correa Rd., Honolulu, HI 96822.

[8] U.S. Geological Survey. 1993. Water resources data Hawaii and other Pacific areas, water year 1993. Water-data Report HI-93-1:78-79. U.S. Geological Survey, 677 Ala Moana Suite, Honolulu, HI 96813.

pelago are intriguing and potentially important. It is not clear how widespread such habitat (and associated high densities of juvenile snappers) may be in Hawaii; present surveys and those of 1967–68 suggest that it represents a minor fraction of all habitat at appropriate depths. Use of the observed mean density of snappers on other habitats (6.6 snappers/km^2) produced an estimate of juvenile standing stock much lower than that derived from catch records. A possible explanation for the discrepancy is that an abundance of snappers use unidentified habitats significantly shallower or deeper than 60–90 m. However, extensive diving in shallower waters, observations from submersibles (Moffitt et al., 1989; Haight et al., 1993), and systematic trawl surveys of deeper waters (Struhsaker, 1973) have not disclosed juveniles in other depth ranges. Conceivably, areas at depths with less than prime habitat for juvenile snappers may support loose, mobile aggregations with large home ranges that are difficult to relocate. As of yet, no such aggregations have been documented.

According to the Kaneohe GIS data (Fig. 5), juvenile snappers occurred within an area of 8 km^2 and showed a median video-based density index of 7; therefore, Kaneohe is likely to support 450 snappers/km^2 (68-fold above mean estimated density) or a total of 3,600 snappers. This finding suggests that recruits from premium habitats like Kaneohe can produce a significant percentage of the MHI juveniles. If Kaneohe snapper abundance values are applied to reconcile the difference between the estimates generated by video densities in nonpremium habitats and those obtained by fishery catches, between 9% and 15% of the MHI habitat would have to be of the premium type to account for the current commercial snapper catch. If recreational catch is considered, a larger fraction of total habitat must be of a premium type. Exploring the actual extent of this habitat and the adult stock's dependence on it should be a management priority and a major focus for future work.

Acknowledgments

We are grateful to Deborah Goebert, Matt McGranaghan, Ross Sutherland, and Everett Wingert for providing expertise helpful in preparing this report. Thoughtful reviews were provided by Wayne Haight, Don Kobayashi, Robert Moffitt, James Parrish, Jeffrey Polovina, and Jim West. The City and County of Honolulu, Department of Wastewater, assisted by providing wastewater discharge data.

Literature cited

Bardach, J. E.
1959. The summer standing crop of fish on a shallow Bermuda reef. Limnol. Oceanogr. 4:77–85

Birkeland, C.
1984. Influence of topography of nearby land massess in combination with local water movement patterns on the nature of nearshore marine communities. UNESCO Reports Mar. Sci. 27:16–31.

Bromwell, K. B.
1992. Assessing the primary biological productivity of Kailua Bay, its influencing streams and 2° treated effluent, through algal biostimulation analysis. Master's thesis, Univ. Hawaii, Honolulu, HI, 33 p.

Buchanan, J. B., and J. J. Moore.
1986. A broad review of variability and persistence in the Northumberland benthic fauna—1971–85. J. Mar. Biol. Assoc. U.K. 66:641–657.

Cyrus, D. P., and S. J. M. Blaber.
1983. The influence of turbidity on fish distribution in Natal estuaries: national oceanographic symposium, Grahamstown (South Africa) Jan. 1983, 7 p. S. Afr. J. Sci. 79(4), p. 156.

DeMartini, E. E., K. C. Landgraf, and S. Ralston.
1994. A recharacterization of the age-length and growth relationships of Hawaiian snapper *Pristipomoides filamentosus*. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-199, 14 p.

DeMartini, E. E., F. A. Parrish, and D. M. Ellis.
1996. Barotrauma-associated regurgitation of food: implications for diet studies of Hawaiian pink snapper, *Pristipomoides filamentosus* (family Lutjanidae). Fish. Bull. 94:250–256.

Eastman, R. J.
1992. IDRISI user's guide. Graduate school of Geography, Clark Univ., Worcester, MA, 82 p.

Ellis, D. M., and E. E. DeMartini.
1995. Evaluation of a video camera technique for indexing abundances of juvenile pink snapper, *Pristipomoides filamentosus*, and other Hawaiian insular shelf fishes. Fish. Bull. 93(1):67–77.

Everhart, W. H., and W. D. Youngs.
1981. Principles of fishery science, 2nd ed. Comstock Publ. Assoc., Ithaca, NY, 349 p.

Fegley, S. R.
1988. A comparison of meiofaunal settlement onto the sediment surface and recolonization of defaunated sandy sediment. J. Exper. Mar. Biol. Ecol. 123:97–113.

Francis, M. P.
1995. Spatial and seasonal variation in the abundance of juvenile snapper (*Pagrus auratus*) in the north-western Hauraki Gulf. N.Z. J. Mar. Freshwater Res. 29:565–579.

Gerber, R., and N. Marshall.
1974. Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll. Limnol. Oceanogr. 19:815–825

Grigg, R. W.
1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. Mar. Ecol. Prog. Ser. 103:25–34

Gulland, J. A.
1983. Fish stock assessment: a manual of basic methods. John Wiley & Sons, Chichester, U.K., 223 p.

Haight, W. R., D. R. Kobayashi, and K. E. Kawamoto.
1993. Biology and management of deepwater snappers of the Hawaiian Archipelago. Mar. Fish. Rev. 55(2):20–27.

Henderson, S. R.
1992. Environmental conditions and sewage effects (or non-effects) around Mokapu Peninsula, Oahu, Hawaii. *In* Proceedings of the seventh international coral reef symposium, Guam 1:249–256.
Johannes, R. E.
1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fishes 3:65–84.
Kleinbaum, D. G.
1992. Logistic regression, a self learning text. Springer-Verlag, New York, NY, 282 p.
Mearns, A. J.
1974. Southern California's inshore demersal fishes: diversity, distribution, and disease as responses to environmental quality. Calif. Coop. Oceanic Fish. Invest. Rep. 17:141–148.
Moffitt, R. B., and F. A. Parrish.
1996. Habitat and life history of juvenile Hawaiian pink snapper, *Pristipomoides filamentosus*. Pac. Sci. 50(4) 371– 381.
Moffitt, R.B., F. A. Parrish, and J. J. Polovina.
1989. Community structure, biomass and productivity of deepwater artificial reefs in Hawaii. Bull. Mar. Sci. 44(2):616–630.
Monaco, M.E., T. A. Lowery, and R. L. Emmett.
1992. Assemblages of U.S. West coast estuaries based on the distribution of fishes. J. Biogeogr. 19(3):251–267.
Nichols, F. H.
1985. Abundance fluctuations among benthic invertebrates in two Pacific estuaries. Estuaries 8(2A):136–144.
Norusis, M. J.
1992. SPSS/PC+ advanced statistics, version 5.0. SPSS Inc., 444 N. Michigan Ave., Chicago, IL 60611, 477 p.
Parrish, F. A.
1989. Identification of habitat of juvenile snapper in Hawaii. Fish. Bull. 87(4):1001–1005.
Parrish, J. D.
1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. Mar. Ecol. Progr. Ser. 58:143– 160.
Ralston, S.
1981. A study of the Hawaiian deepsea handline fishery with special reference to the population dynamics of opakapaka, *Pristipomoides filamentosus* (Pisces: Lutjanidae). Ph.D. diss., Univ. Washington, Seattle, WA, 205 p.
1987a. Mortality rates of snappers and groupers. *In* J. J. Polovina and S. Ralston (eds.), Tropical snappers and groupers: biology and fisheries management, p. 375–404. Westview Press, Boulder, CO.
1987b. Biological constraints on production and related management issues in the Hawaiian deepsea handline fishery. *In* R. W. Grigg and K. Y. Tanoue (eds.), Proceedings of the second symposium on resource investigations in the northwestern Hawaiian Islands, May 25–27, 1983, p. 248–264. Univ. Hawaii, Honolulu, HI, UNIHI-SEAGRANT-MR-84-01 Vol. 1.
Ralston, S., and J. J. Polovina.
1982. A multispecies analysis of the commercial deep-sea handline fishery in Hawaii. Fish. Bull. 80(3):435–448.
Siegel, S., and N. Castellan Jr.
1988. Nonparametric statistics for the behavioral sciences, 2nd ed. McGraw-Hill, New York, NY, 399 p.
Smith, S. V., K. E. Chave, and D. T. O. Kam.
1973. Atlas of Kaneohe Bay: a reef ecosystem under stress. UNIHI-SEAGRANT-TR-72-01 Honolulu, Hawaii, 128 p.
Struhsaker, P.
1973. Contribution to the systematics and ecology of Hawaiian bathyal fishes. Ph.D. diss., Department of Zoology, Univ. Hawaii, Honolulu, HI, 482 p.
Sudo, H., R. Ikemoto, and M. Azeta.
1983. Studies on habitat quality evaluation of red seabream youngs in Shijiki Bay. Bull. Seikai Reg. Fish. Res. Lab. 59:71–84.
Tito de Morais, L., and J. Y. Bodiou.
1984. Predation on meiofauna by juvenile fish in a western Mediterranean flatfish nursery ground. Mar. Biol. 82:209–215.
U.S. Army Corps of Engineers.
1984. Moloka'i Coastal Resource Atlas. Manoa Mapworks DACW- 84-83-M-0660, 357 p. U.S. Army Corps of Engineers, Honolulu, HI.

Application of high-breakdown robust regression to tuned stock assessment models

Victor R. Restrepo
Rosenstiel School of Marine and Atmospheric Science, Cooperative Unit for Fisheries Education and Research
University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149
E-mail address: vrestrepo@rsmas.miami.edu

Joseph E. Powers
National Marine Fisheries Service, Southeast Fisheries Science Center
75 Virginia Beach Drive, Miami, Florida 33149

Abstract.—Many tuned assessment models, such as sequential population analysis and nonequilibrium production models, are cast in the form of least-squares minimization routines. It is well known that outliers can substantially alter the results of least-squares methods. Indeed, in the process of conducting stock assessments, much time and effort are often spent in discussing the merits of individual data points and in evaluating the impact that including or excluding them has on the perceived stock status. Unfortunately, straight-forward statistical tests for detecting outliers have been developed only for univariate statistics or for the simplest of linear models and are generally useful to test for a single outlier only. In this paper, we apply a high-breakdown robust regression technique, least trimmed squares, to two assessment models using North Atlantic swordfish and West Atlantic bluefin tuna as examples. We illustrate how robust regression can be used as an initial step in statistically detecting outliers before the more efficient least-squares minimization can be used.

Manuscript accepted 30 July 1996.
Fishery Bulletin 95:149–160 (1997).

Tuned stock assessment models are statistical methods that analyze time series of fishery catch data in conjunction with auxiliary information (indices of relative abundance, fishing effort, etc.) to yield estimates of stock abundance and exploitation rates over time. Such methods are widely used today by stock assessment working groups throughout the world because they provide an objective and statistically defensible way to assess the status of stocks and to derive management advice. The two primary methods are sequential population analysis (SPA: Fournier and Archibald, 1982; Deriso et al., 1985; Pope and Shepherd, 1985; Kimura, 1989; Methot, 1990; Powers and Restrepo, 1992; Gavaris[1]) and nonequilibrium production models (Pella and Tomlinson, 1969; Hilborn, 1990; Hilborn and Walters, 1992; Prager, 1994). SPA's are typically age structured and production models are not, although there are exceptions to this generalization in the references just cited. Both types of methods, however, share the commonality of often being cast as nonlinear least-squares minimization problems.

Despite efforts to standardize all steps involved in a stock assessment (from data collection, preparation of model inputs, to running the models), stock assessments are rarely automated and, more often than not, generate controversy. In our experience with different fora, a common cause for controversy is as follows: various data sets are presented to a working group and then the group collectively decides on the sets of data and model assumptions to be used. The consensus selection is typically termed the "base case." Individual data points are then scrutinized for exclusion from further analyses to determine the robustness of the overall assessment to the sensitivity changes. This partial "sensitivity analysis" can, in practice, be undesirable because perceptions of what results ought to be like may influence which data or data points are scrutinized and thus generate controversy; not every working group participant has the same perception. The lack of an a priori objective selection process could lead working groups astray (Restrepo and Powers, 1995). A so-

[1] Gavaris, S. 1988. An adaptive framework for the estimation of population size. Can. Atl. Fish. Sci. Adv. Comm. (CAFSAC) Res. Doc. 88/29, 12 p. Biological Station, Department of Fisheries and Oceans, St. Andrews, New Brunswick, Canada EOG 2X0.

lution to this problem lies in a method that would objectively identify—and deal with—"outliers."

Statistical tests have been developed for identifying outliers (see Barnett and Lewis, 1994), but most of the straight-forward approaches can only deal with a few outliers in univariate analyses or in linear regression. High-breakdown robust regression methods (Rousseeuw, 1984; Rousseeuw and Leroy, 1987) hold promise for addressing the issue, as suggested by several recent papers in fisheries literature (e.g. Chen et al., 1994; Chen and Paloheimo, 1994). The goal of high-breakdown robust regression is to provide model estimates that are insensitive to contamination (up to 50%) by outliers and thus will serve to identify outlying observations. However, most robust regression applications in fisheries science (Chen et al., 1994; Chen and Paloheimo, 1994) and in statistics literature have been developed for linear problems (but, see Stromberg, 1993). In this study we seek to illustrate the application and usefulness of this tool by using two nonlinear examples: a nonequilibrium production model for North Atlantic swordfish, *Xiphias gladius,* and a sequential population analysis for West Atlantic bluefin tuna, *Thunnus thynnus*. Both stocks are assessed by the Standing Committee on Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT). The analyses presented here are illustrative and are not intended to replace those of the SCRS.

Methods

Assessment models

Assuming a normal (Gaussian) error structure, the typical tuned assessment method minimizes the squared deviations (residuals, r) between observed and predicted indices of abundance:

$$\min \sum_{i=1}^{m} \sum_{j=1}^{n_i} (I_{ij} - \hat{I}_{ij})^2 = \min \sum_{i=1}^{m} \sum_{j=1}^{n_i} (r_{ij}^2), \qquad (1)$$

for m indices, each with n_i observations. The prediction of each index, $\hat{I}_{ij}$, comes from a population model, such as a surplus production model or a sequential population analysis. Alternatively, the minimization can be made in terms of observed and predicted catches or in terms of observed and predicted fishing effort. Note that some maximum-likelihood approaches do not make the normal error assumption (e.g. Fournier and Archibald, 1982); we focus on those approaches that are in a least-squares framework or that can be transformed to one, which include iteratively reweighted least squares and some forms of maximum likelihood.

In this paper, we give robust regression examples using two population models. A detailed explanation of these methods is beyond the scope of this paper and readers are referred to the citations given below. The surplus production model corresponds to a Schaeffer (logistic) form, fitted as nonequilibrium time series by using the continuous time method presented by Prager (1994). This method estimates parameters describing the carrying capacity, rate of intrinsic population growth, initial biomass, and catchability coefficients that best explain observed time series of relative abundance according to the criterion in Equation 1. The sequential population analysis corresponds to a tuned virtual population analysis method known as ADAPT, an age-structured assessment framework popular in the east coast of North America. Details on ADAPT can be found in Powers and Restrepo (1992, 1993), Punt (1994), and Gavaris.[1] ADAPT estimates age-specific fishing mortality rates in the last year of data and catchability coefficients that satisfy Equation 1, while forcing cohorts to conform to exponential survival through time:

$$N_{a+1,y+1} = N_{a,y} e^{-Z_{a,y}},$$

where N denotes stock size in numbers, Z denotes instantaneous total mortality, and a and y are subscripts for age and year.

Data sets

The data set used with the nonequilibrium production model is for North Atlantic swordfish as employed by ICCAT in its 1994 assessment (ICCAT, 1995). This data set consists of total landings (in weight) for the period 1950–93 and of a single standardized longline series of catch per unit of effort (CPUE, used as a measure of relative abundance), spanning the period 1963–93 (Table 1). After a series of sensitivity tests, ICCAT assumed in its "base case" analysis that the initial biomass in 1950 was a known quantity, equal to 0.875 times the stock's carrying capacity. Thus, 3 parameters were estimated: carrying capacity, intrinsic rate of growth, and a constant of proportionality (q) relating the series of relative abundance (X) to absolute biomass units (B). The minimization of Equation 1 was done in log scale, i.e. $I_{ij} = \ln(X_{ij})$ and $\hat{I}_{ij} = \ln(qB_j)$.

The data for the SPA is for West Atlantic bluefin tuna, also as employed by ICCAT in its 1994 base case assessment (ICCAT, 1995). It consisted of catch

Table 1

North Atlantic swordfish, *Xiphias gladius*, data used for the nonequilibrium production model (from ICCAT, 1995). Relative abundance is in Kg/1,000 standard hooks, standardized from Canadian, Japanese, Spanish, and U.S. longliners. t = metric tons.

Year	Landings (t)	Relative abundance	Year	Landings (t)	Relative abundance
1950	3,646	—	1973	6,001	—
1951	2,581	—	1974	6,301	—
1952	2,993	—	1975	8,776	421.69
1953	3,303	—	1976	6,587	353.66
1954	3,034	—	1977	6,352	393.92
1955	3,502	—	1978	11,797	649.61
1956	3,358	—	1979	11,859	338.57
1957	4,578	—	1980	13,527	430.69
1958	4,904	—	1981	11,138	310.18
1959	6,232	—	1982	13,155	356.96
1960	3,828	—	1983	14,464	287.88
1961	4,381	—	1984	12,753	286.12
1962	5,342	—	1985	14,348	265.94
1963	10,189	1,258.10	1986	18,447	255.54
1964	11,258	467.29	1987	20,234	217.30
1965	8,652	294.86	1988	19,614	207.62
1966	9,338	273.50	1989	17,299	196.90
1967	9,084	320.22	1990	15,865	199.20
1968	9,137	269.55	1991	15,224	194.02
1969	9,138	233.95	1992	15,593	182.55
1970	9,425	274.25	1993	16,977	172.27
1971	5,198	—			
1972	4,727	—			

at age from 1970 to 1993 for ages 1 to 10^+ (Table 2), and of 7 indices of relative abundance assumed to track different segments of the population (Table 3; see Fig. 4). A number of assumptions were made and these can be found in Appendix BFTW-2 of ICCAT (1995). The parameters estimated were 7 constants of proportionality relating each index of relative abundance to absolute biomass or numbers and 4 fishing mortalities in 1993 (for ages 2, 4, 6, and 8).

We reiterate that we chose the same data sets and model structures as those in ICCAT (1995) for illustrative purposes. It may be worthwhile to investigate the results of robust regression techniques applied to alternative data (e.g. indices obtained with a different standardization procedure) or to formulations (e.g. different assumptions about known quantities and other constraints).

Robust regression

Several robust minimization criteria discussed in Rousseeuw and Leroy (1987) have been applied to fisheries data (see Chen et al., 1994). In contrast with the method of least squares, the goal of these techniques is to moderate the influence of outliers in the parameter fitting process (Eq. 1). Of particular interest to us are the so-called "high-breakdown" methods that are insensitive to up to 50% contamination by outliers, because they can effectively be used as an objective method to identify outliers.

Two high-breakdown robust regression methods are least median squares (LMS) and least trimmed squares (LTS). LMS minimizes the median of the squared residuals and LTS minimizes the sum of the lowest xn squared residuals, where x is a fraction (less than 1.0 to 0.5) defined by the user. The results of an LMS regression and an LTS regression with a 50% trim are essentially very similar, although the LTS one is statistically more efficient (Rousseeuw and Leroy, 1987). In our initial experimentation with fisheries assessment models, we found that the LTS minimum was somewhat easier to find (the LMS could sometimes not converge, indicating that a large number of restarts may be required). Therefore, we limited our investigation to the LTS minimization criteria discussed below. This can be either

$$LTS_1 = \sum_{i=1}^{m} \min \sum_{j=1}^{n_i/2+1} (r^2)_{j:n_i} \tag{2}$$

or

$$LTS_2 = \min \sum_{i=1}^{m} \sum_{j=1}^{n_i/2+1} (r^2)_{j:n_i}, \tag{3}$$

Table 2

West Atlantic bluefin tuna, *Thunnus thynnus*, catch at age data (in numbers) used for the sequential population analysis (from ICCAT, 1995).

	Age									
Year	1	2	3	4	5	6	7	8	9	10+
1970	64,886	105,064	127,518	21,455	3,677	914	176	172	535	3,726
1971	62,998	153,364	38,360	46,074	672	1,673	2,109	1,350	1,133	5,957
1972	45,402	98,578	33,762	3,730	3,857	118	569	576	261	5,519
1973	5,105	74,311	30,482	7,161	2,132	1,451	953	1,544	555	4,444
1974	55,958	20,056	21,094	6,506	3,170	683	916	913	1,081	12,508
1975	43,556	148,027	8,328	11,963	821	547	317	671	1,651	9,472
1976	5,412	19,781	72,393	2,910	2,899	344	206	1,168	558	14,033
1977	1,274	22,419	9,717	32,139	4,946	3,633	957	513	1,109	13,532
1978	5,133	10,863	20,015	6,315	10,530	4,061	655	472	341	11,982
1979	2,745	10,552	16,288	14,916	3,448	3,494	2,612	599	557	12,283
1980	3,160	16,183	11,068	8,881	2,866	2,982	5,533	3,454	1,061	12,213
1981	6,087	9,616	16,541	5,244	6,023	3,721	2,884	3,211	2,764	10,621
1982	3,528	3,729	1,654	498	342	751	477	519	896	3,077
1983	4,173	2,438	3,268	894	866	911	1,402	1,353	1,039	5,628
1984	868	7,504	1,848	2,072	2,077	1,671	594	759	1,091	4,574
1985	568	5,523	12,310	2,814	4,329	4,019	1,024	612	698	5,603
1986	563	5,939	7,135	3,442	1,128	1,726	931	520	345	5,335
1987	1,513	13,340	9,137	5,491	4,385	2,318	1,566	1,251	1,014	3,856
1988	4,850	9,149	11,745	3,933	4,144	4,220	2,258	1,631	1,600	4,555
1989	787	12,877	1,679	3,815	1,713	2,082	2,677	1,864	1,461	5,356
1990	2,368	4,238	17,958	1,947	2,747	1,825	1,629	2,388	1,522	4,253
1991	3,327	14,533	10,761	2,924	1,650	2,166	2,347	1,946	1,915	4,485
1992	420	5,985	1,997	711	1,425	737	1,916	1,870	1,323	4,383
1993	329	1,130	5,215	3,689	2,089	1,883	1,598	2,456	1,479	2,922

where the notation $j{:}n_i$ indicates that the squared residuals are sorted in ascending order from j=1 to n_i; note that $n_i/2+1$ is actually an integer value equal to $n_i/2$ when n_i is even and equal to $n_i/2+1$ when n_i is odd. Equations 2 and 3 are two different minimization objectives that differ in the way they treat multiple series of relative abundance data. In Equation 2, the trimmed sums of squared residuals are computed separately for each index and then added to the objective function being minimized. Thus, the individual indices are de facto given equal weighting. In Equation 3, the trimming is done over all available data points, regardless of which relative abundance series they belong to. Thus, the LTS_1 formulation forces each available series to contribute to the objective function, whereas the LTS_2 formulation could plausibly eliminate indices that fit very poorly in comparison with the others. An analogous distinction can be made for the LS fit by giving either equal weight to all available data series (as in Eq. 1) or by assigning weights to each series in proportion to their mean squared errors. The latter has often been accomplished by means of iterative reweighting (Powers and Restrepo, 1992) or maximum likelihood (Punt, 1994).

Algorithms for high-breakdown robust regression are notoriously computation-intensive, even in the simplest univariate linear regression case (Rousseeuw, 1984; Rousseeuw and Leroy, 1987; Steele and Steiger, 1986). A typical algorithm for a linear robust regression with p parameters goes like this: For a large number of times, s, select p data points, do a least-squares regression (LS) and compute the corresponding robust objective function (e.g. sum of trimmed squares) for the complete data set. The LTS solution is given by the parameter estimates and results in the lowest robust objective function value. In the linear case, the value of s is chosen such that, for a given fraction of data contamination and a given p, at least one of the s subsamples is not contaminated (Rousseeuw and Leroy, 1987). The choice of s in the nonlinear case is not clearcut. However, in the linear case the values of s grow very rapidly with p and percent contamination; therefore many available algorithms set $s = 3{,}000$ for $p > 9$ (Rousseeuw and Leroy, 1987). Similar values were used here for the nonlinear case.

Algorithms for nonlinear robust regression are rare, owing partly to the increased computational

Table 3

West Atlantic bluefin tuna, *Thunnus thynnus*, relative abundance indices (from ICCAT, 1995). The larval index is in relative biomass units, while all others are in relative numbers. The numbers below each index label are the ages or range of ages that each index is assumed to represent. TL = tended line, LL = longline, RR = rod and reel, GOM = Gulf of Mexico, NWA = Northwest Atlantic.

Year	Canada TL 10^+	Japan LLGOM 10^+	Japan LLNWA 1–9	Larval GOM 8^+	US LLGOM 8^+	US RR 8^+	US RR 1–5
1974	—	1.4670	—	—	—	—	—
1975	—	1.0200	—	—	—	—	—
1976	—	0.8960	0.8134	—	—	—	—
1977	—	0.6700	1.7822	1.7704	—	—	—
1978	—	0.9350	1.4621	4.2341	—	—	—
1979	—	0.9380	0.5476	—	—	—	—
1980	—	1.5130	1.0327	—	—	—	1.2109
1981	2.3489	0.5610	1.4812	0.9575	—	—	0.1274
1982	2.1095	—	0.7121	1.1008	—	—	1.3417
1983	1.5621	—	0.5022	0.8977	—	2.4703	0.7816
1984	1.0718	—	0.8527	0.4750	—	1.0949	—
1985	0.5131	—	0.9967	—	—	1.0483	0.5366
1986	0.6157	—	0.5725	0.1897	—	0.7324	0.9995
1987	0.3991	—	1.1490	0.3236	1.7544	0.6933	1.2138
1988	0.6271	—	0.8773	1.4146	0.6842	1.3195	1.6059
1989	0.4561	—	0.7417	0.5803	1.0526	0.6808	1.3339
1990	0.2965	—	0.7754	0.3446	1.1404	0.6204	0.7331
1991	—	—	0.7523	0.2652	1.5614	0.7694	1.3277
1992	—	—	1.8813	0.4464	0.5263	0.8727	0.7968
1993	—	—	1.0675	—	0.2807	0.6981	0.9912

requirements. Although the LS solutions for the linear case (as described in the previous paragraph) can be accomplished with simple matrix manipulations, nonlinear LS solutions require iterative computations. Stromberg (1993) presented a multistage algorithm for nonlinear regression that is similar to the one outlined above, succeeded by a direct minimization of the robust objective function by using the simplex search of Nelder and Mead (1965). Building upon Stromberg's ideas, we reviewed algorithms for an LTS_1 solution to the bluefin tuna SPA. On the basis of these results and the work of Stromberg (1993), we adopted the algorithm below but acknowledge that there are many other possible fruitful options to be explored, such as "simulated annealing" (Corana et al., 1987). Our algorithm uses the fact that the simplex search of Nelder and Mead (1965) requires $p+1$ starting guesses, denoted by v vertices, for each of the p parameters being estimated.

1 Find the LS estimate for the entire data set. The estimates $(p)_{LS}$ are used as starting guesses for step 2.
2 Repeat s times:
   a) Set initial parameter guesses at random from within 10 times the $(p)_{LS}$ estimates from step 1.
   b) Find the LTS estimates for the complete data set by using the starting values from step 2a.
   c) Restart step 2b until the objective function (either Eq. 2 or Eq. 3) does not change appreciably.
   d) Save the parameter estimates corresponding to the $(p+1)_{LTS}$ parameter sets with the lowest objective function value.
3 Initialize the v vertices for the simplex search with the best $(p+1)$ parameter sets from the s solutions from step 2 and find the LTS estimate for the entire data set. As in step 2, carry out restarts as needed.

This algorithm is a direct robust minimization search that is initialized s times from a Monte Carlo grid centered around the LS solution. It is computationally intensive, but this seems necessary given the multi-modal nature often encountered in the LTS or LMS objective function. For this study we used s = 500. For both the swordfish nonequilibrium production model and the bluefin tuna SPA analyses, step 2 involved 5 restarts on average and thus made the total number of minimizations greater than 2,500. It should be noted that this search algorithm does not guarantee that a global minimum LTS solution is going to be found. Therefore, we favor mul-

tiple replicates and restarts so that there is some confidence that the solution is globally minimal. At this point we have no firm guidance about the tradeoffs between the number of replicates (s) and the number of restarts other than to say that replicates are probably more important than restarts. For example 500 replicates with 5 restarts seems preferable to 25 replicates with 100 restarts.

Dealing with outliers

Aside from biological or fishery considerations, statistical outliers are data points whose residuals, scaled by the dispersion of errors,

$$\frac{r_{ij}}{\sigma}$$

are far from the mean scaled residual. For the simple LS minimization (Eq. 1), the overall dispersion of the residuals is the mean squared error (MSE),

$$\sigma = \sqrt{\frac{1}{\sum_{i=1}^{m} n_i} \sum_{i=1}^{m} \sum_{j=1}^{n_i} (r_{ij}^2)}.$$

For the LTS regression, the dispersion is similarly computed as a robust measure of average dispersion (σ_i for index i in Eq. 2 or σ for all data points in Eq. 3):

$$\sigma_i = 3.7444 \sqrt{\frac{1}{n_i} \sum_{j=1}^{n_i/2+1} (r^2)_{j:n_i}}$$

for LTS_1, Eq. 2, or

$$\sigma = 3.7444 \sqrt{\frac{1}{\sum_{i=1}^{m} n_i} \sum_{i=1}^{m} \sum_{j=1}^{n_i/2+1} (r^2)_{j:n_i}}$$

for LTS_2, Eq. 3.

The constant 3.7444 is a correction factor used to achieve consistency with normal error distributions (Rousseeuw and Leroy, 1987). As a rule of thumb, Rousseeuw and Leroy (1987) suggest that absolute values of scaled residuals larger than 2.5 can be treated as statistical outliers. Owing to the small number of observations in some of our data series, we use a threshold based on the t-distribution with $\alpha = 0.01$ and $n-1$ degrees of freedom. After obtaining the LTS estimates, we carried out a new least-squares minimization excluding from the analyses any absolute scaled residuals greater than the corresponding critical value. We refer to this final result as the "trimmed LS" solution.

Results

Swordfish nonequilibrium production model

The swordfish data represent a simple example with a single index. Nevertheless, there are several very large deviations between the observed and predicted index values, when the traditional least-squares (LS) solution to the nonequilibrium production model fit is computed (Fig. 1). Indeed, these deviations have generated considerable debate (ICCAT, 1995). Therefore, we applied the robust regression techniques of the LTS algorithm and the trimmed LS method of outlier detection to this example. The LTS solution (with a 50% trim) was computed 500 times with 5 restarts each. There did not appear to be problems of multiple minima with this example because vir-

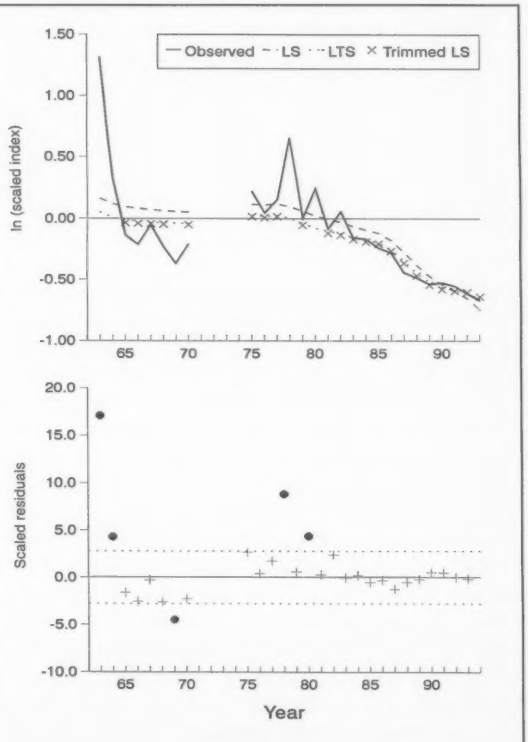


Figure 1

Biomass index values for North Atlantic swordfish using least squares (LS), least trimmed squares (LTS), and trimmed least squares (Trimmed LS). The top panel shows observed and predicted index values. The bottom panel shows the scaled residuals from the LTS fit compared with the critical value for the outlier detection criterion (dashed lines); solid circles are those data points considered to be outliers and not included in the final trimmed LS solution.

tually all of the 500 solutions converged to the same value. The outlier detection criteria identified five of the original 27 data points (19%), all of which occurred before 1981 (Fig. 1). Predicted index values with both the LTS and trimmed LS solutions were higher than the LS predictions prior to the late 1980's and lower than LS predictions in recent years (Fig. 1).

Predicted relative biomass values with either the LTS or trimmed LS solutions are higher than the initial LS solution (ICCAT, 1995), particularly in the 1990's (Fig. 2) and suggest less of a decline in the population. Absolute biomass predictions with the LTS method were generally higher than those from the initial LS solution, whereas trimmed LS solutions were lower (Fig. 2). The trimmed LS solution results in biomass levels that are lower than those in the other two methods; however, the decline over the time series is less. Biomass projections were made under two strategies: 1) a recovery strategy in which future fishing mortality rate was fixed at the value that would produce maximum sustainable yield and 2) a status quo strategy in which the fishing mortality would be fixed at the 1993 level. The LTS and trimmed LS projections indicate that both recovery and decline is not as rapid as that predicted from the initial LS solution (Fig. 2).

The robust regression techniques applied here tend to provide a better fit to the index data points in recent years at the expense of the data points in the earlier years of the series. Indeed, several of the points identified through the outlier detection process were those data points for which there was much debate regarding variability and bias (ICCAT, 1995). However, some of the data points identified here were not identified by ICCAT (1995); therefore, we reemphasize the point that the selection of outliers should be based on objective criteria.

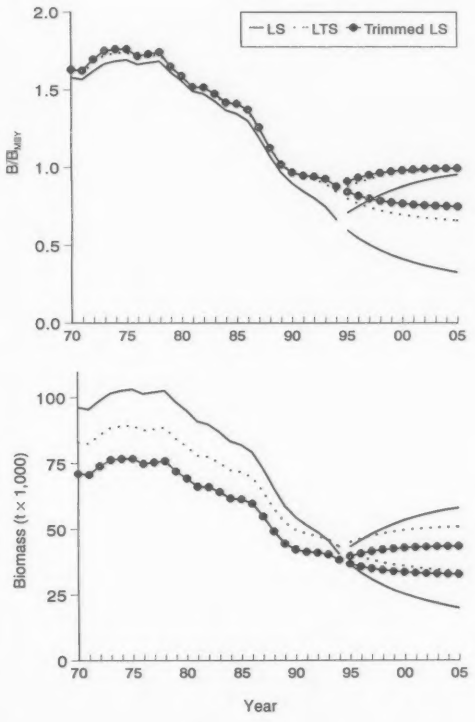


Figure 2

Predicted biomass relative to biomass at maximum sustainable yield (B/B_{MSY}, top panel) and absolute biomass (bottom panel) resulting from LS, LTS, and trimmed LS solutions. The left side of the graphs show the production model estimates. The right sides of the graphs are projections made with the fishing mortality rate at maximum sustainable yield (F_{MSY}) and with the fishing mortality rate in 1993 (F 93). Ascending limbs were projected by using F_{MSY}, descending limbs by using F 93.

Bluefin tuna SPA

As mentioned before, a high-breakdown robust regression objective function can possess multiple minima. Figure 3 illustrates this point with the LTS_1 objective function plotted around ± 50% of the final estimate for one of the parameters, while all other parameter values were fixed at their solution. The figure highlights the need for an exhaustive search owing to the multimodal nature of the response surface.

Figure 4 shows the observed indices of relative abundance in the first column, the scaled residuals

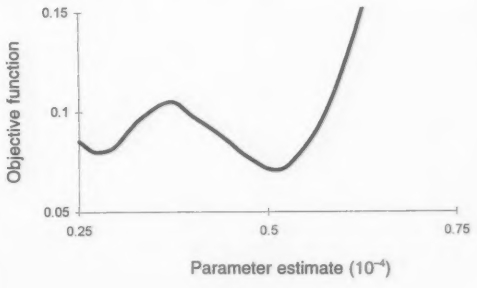


Figure 3

Trimmed squares objective function (Eq. 2) plotted around the solution for one of the parameters estimated in the bluefin tuna sequential population assessment (catchability for the U.S. rod and reel large fish index, Table 3). The plot shows that multiple local minima can occur in robust regression problems.

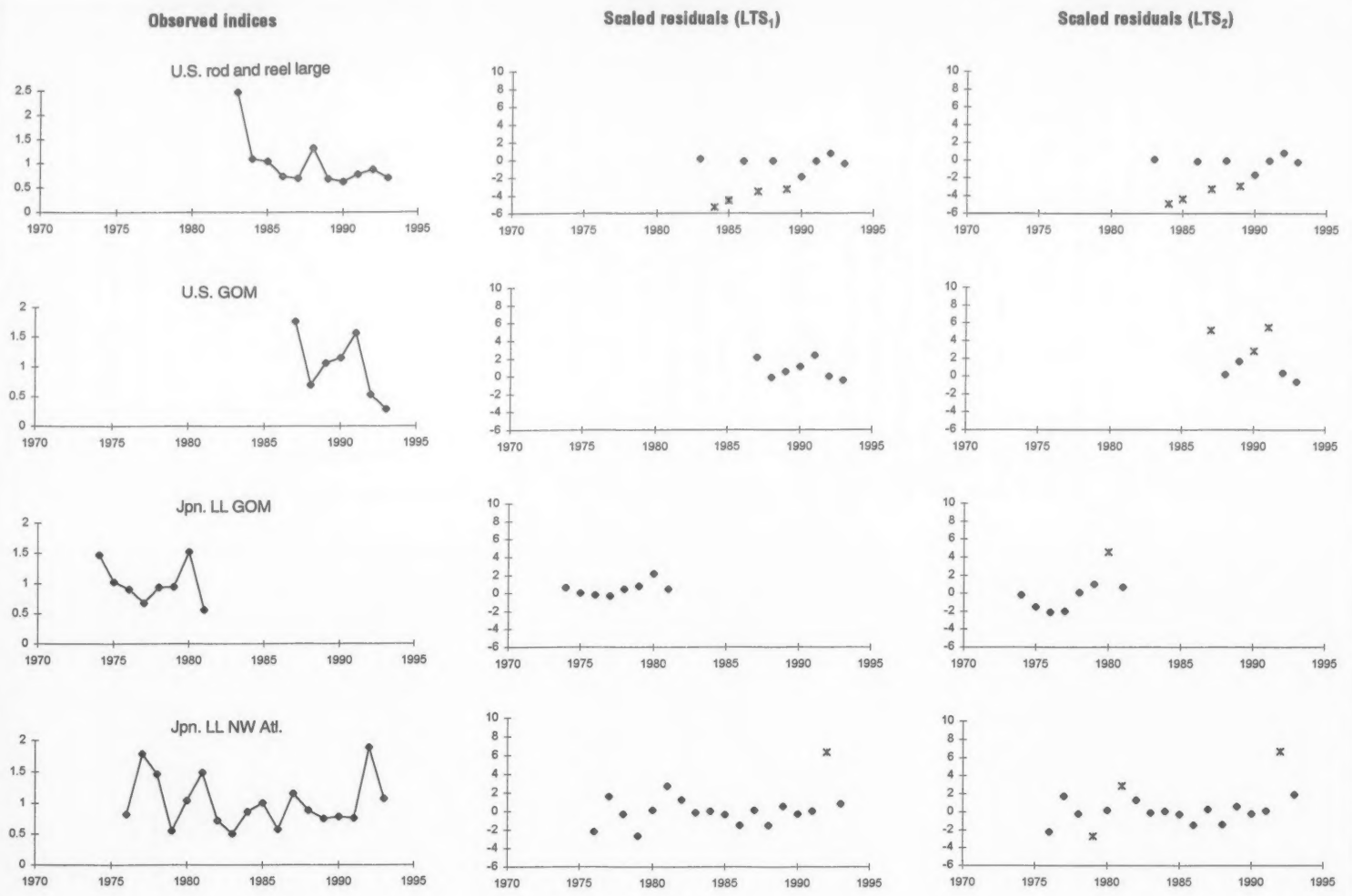


Figure 4

Results from the bluefin tuna sequential population analyses using least trimmed squares (LTS) regression. The left-hand column shows the seven available indices of relative abundance (see Table 3). The middle and right-hand side columns show the scaled residuals resulting from the minimizations with Equations 2 and 3, respectively. Crossed symbols identify statistical outliers at the 1% significance level.

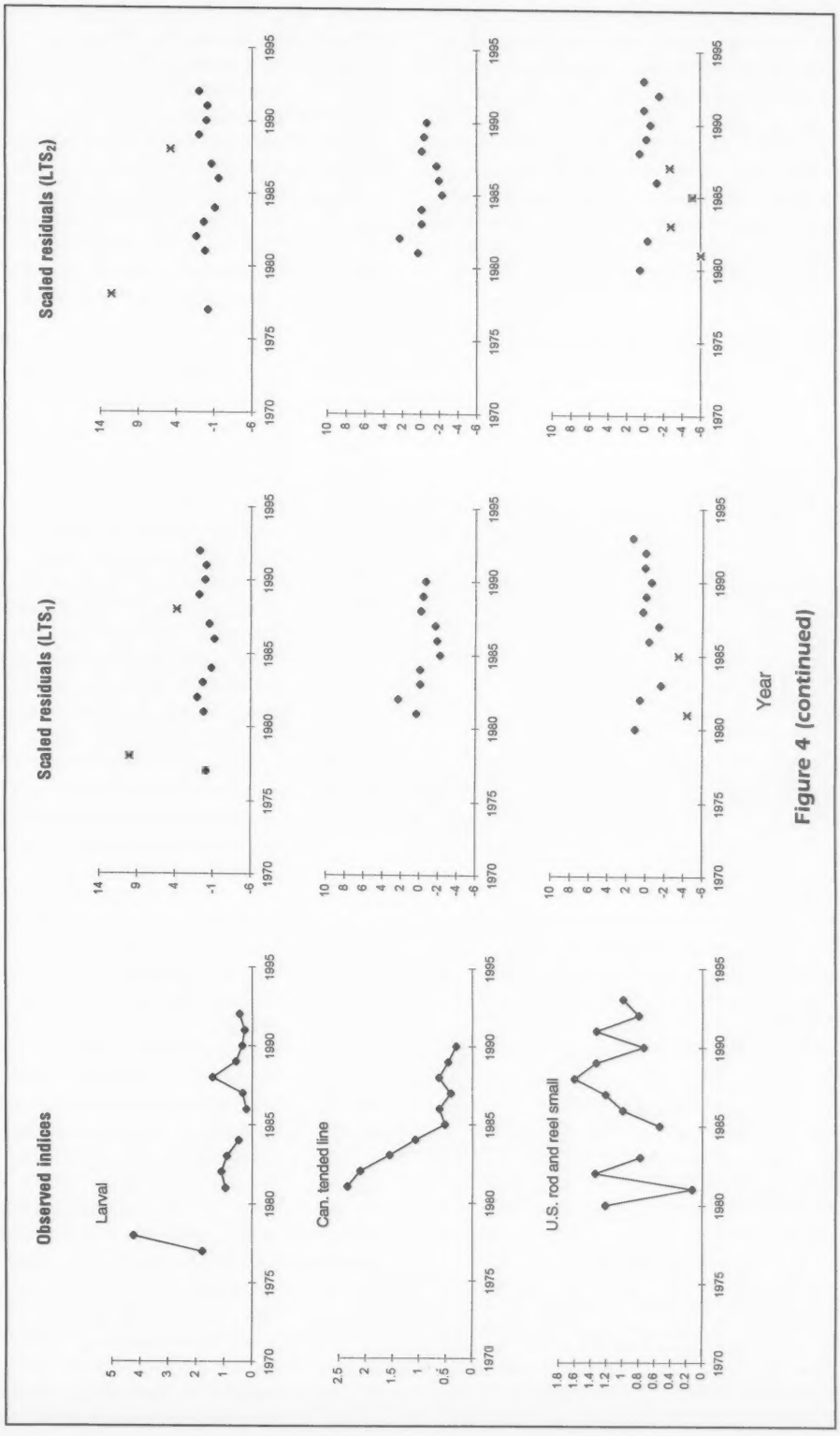


Figure 4 (continued)

from the LTS_1 fit (second column), and the LTS_2 fit (last column). The open symbols indicate which data points were identified as outliers according to the *t*-test criterion mentioned previously. The LTS_1 regression, which gives equal consideration to all index series, identified 9 outliers (11% of the total index data points). The LTS_2 approach, which gives more weight to the better-fitting series, identified the same 9 observations as outliers, and an additional 8 (21% of the total number of data). The 1978 estimate from the larval index stands out as a particularly large outlier (Fig. 4). But perhaps more importantly in terms of the effect on the SPA results, the 1992 data point for the Japanese Northwest Atlantic longline index, is also identified as a large outlier. That is, because of the convergence properties of the ADAPT approach, the more recent data tend to have a larger impact on the estimates of current stock status.

Figure 5 shows the estimated stock size trajectories for 3 age groupings that ICCAT assessments focus on: small fish (ages 2 to 5), medium fish (ages 6 and 7), and spawners (ages 8 and older). The solid line without symbols represents the initial LS solution (Eq. 1), as in the 1994 ICCAT assessment. The 2 dashed lines with symbols (virtually indistinguishable from each other) represent the final trimmed LS solutions, i.e. after removal of the outliers identified in Figure 4. Note that all the stock size estimates are identical in the first half of the time series, owing to the convergence properties of the SPA. Differences in 1990's stock size estimates before and after trimming are most notable for small and medium bluefin tuna (Fig. 5). For this example, the final trimmed LS solutions estimate lower current stock sizes (Fig. 5) and correspondingly higher current exploitation rates (not shown).

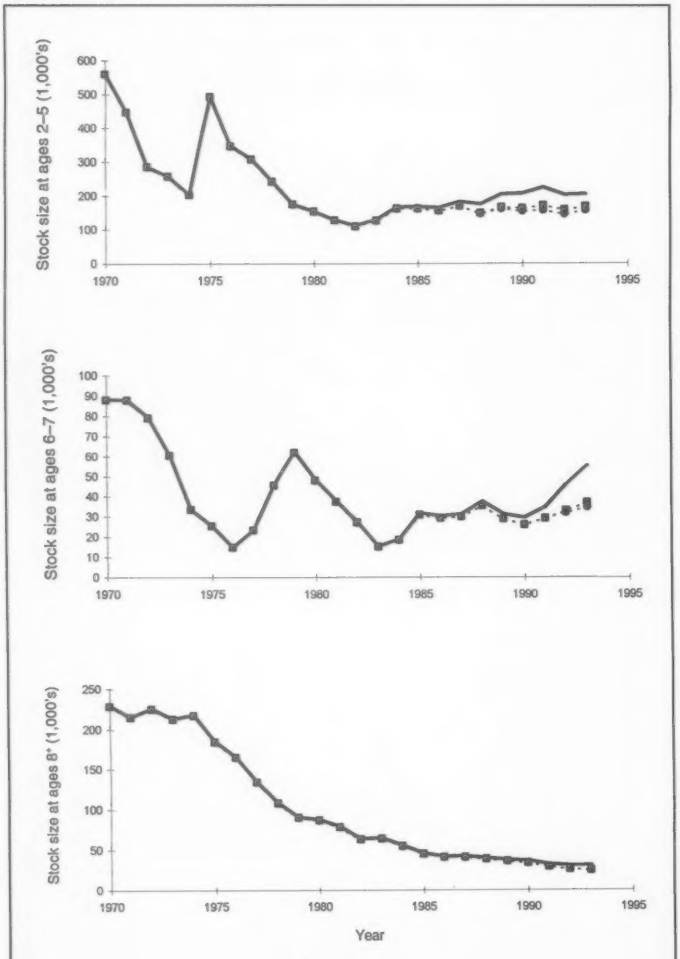


Figure 5

Bluefin tuna stock size estimates for 3 groups of ages. The solid line represents the estimates from the least-squares solution with all the available data, as in the ICCAT assessment. The dashed lines show the least squares estimates after removal of the data points identified as outliers in Figure 4. Squares = after minimization with Equation 2; circles = after minimization with Equation 3. Squares and circles overlap.

The impact that these differences in the estimates have on management recommendations can be appreciated in Figure 6, which shows a 10-year projection of the stock's spawning biomass at two levels of constant landings considered by ICCAT. These projections were made by using the same assumptions as those in the assessment (Appendix BFTW-2 in ICCAT, 1995): essentially, that recruitment is constant after a certain parental biomass level and that the 3 most recent recruitment values from the SPA are poorly estimated and are replaced by the geometric mean recruitment from past years. The top panel in Figure 6 is a projection made by assuming 2,000 metric tons (t) landings after 1993: the lower panel assumes 2,660 t landings after 1993. The solid lines represent the LS solution as in the ICCAT assessment, and the dashed lines represent the LS solutions after trimming (squares for results from the LTS_1 solution and circles for results from the LTS_2 solution). The projections made without removing outliers

are optimistic and suggest a continued increase in parental biomass even at the higher level of landings. The projections made after trimming, on the other hand, are less optimistic. These suggest a more modest increase in spawning biomass at the 2,000 t level of landings, or a decline in spawning biomass after 7 years of 2,660 t landings (Fig. 6).

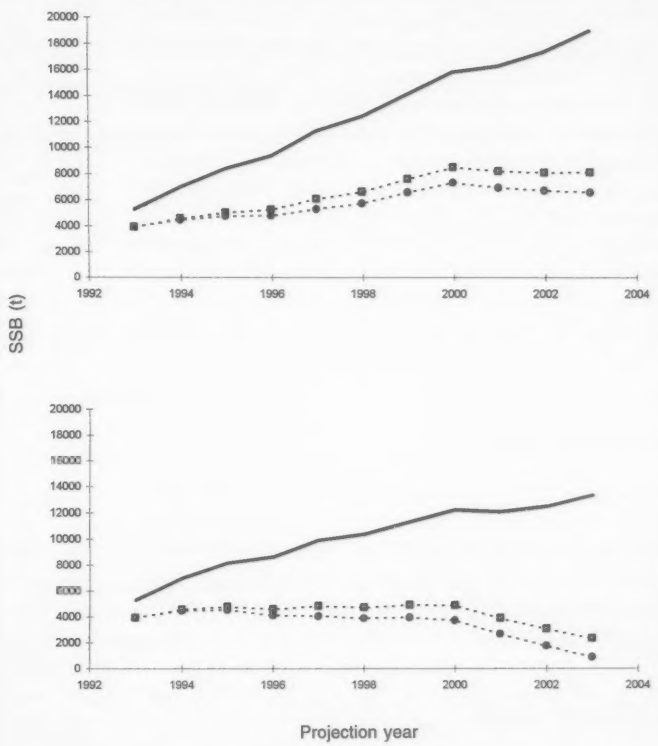


Figure 6

Bluefin tuna spawning stock size projections at two levels of constant landings: 2,000 metric tons (t) (top panel), and 2,660 t (bottom panel). Lines and symbols are the same as those in Figure 5. SSB = spawning stock biomass.

Discussion

The robust regression methods as applied to tuned population assessment models may be helpful in several ways. The methods can be used as an alternative minimization criterion to obtain estimates of the population parameters. They can also be used to identify outliers for elimination from subsequent fitting. In either case, much of the subjectivity that can enter discussions about individual data points during working group meetings would be eliminated. The latter aspect (identification and elimination of outliers) is especially useful because, after elimination of the outliers, one can then go on and conduct the normal bootstrap (Punt, 1994) or Monte Carlo (Restrepo et al., 1992) analyses used to evaluate uncertainty in the estimates. The robust regression methods could be used to screen the outliers, and then the other methods could be used to estimate variability and to project the population status under different management scenarios. Presently, computation time would preclude incorporating bootstrap or Monte Carlo techniques directly into the LTS search. Removing outliers should, also, have a moderating effect on the so-called retrospective patterns (Sinclair et al., 1990), some of which are caused by outliers in the indices (ICES, 1995).

It is important to keep in mind a point of caution when removing statistical outliers from an assessment. Observations that appear to be outliers are so in the overall context of data-model. That is, it is possible that a data point is considered as either an outlier or not, depending on the model formulation, constraints, etc. For example, if the bluefin tuna indices of abundance had been considered to be log-normally distributed instead of normally-distributed, the LTS regression may have identified more or fewer observations as outliers. A related point is that we do not advocate rushing to eliminate outliers automatically from stock assessments. Instead, a first step should be to look into reasons why such observations may seem like outliers, e.g. undetected transcription errors or environmental influences that were not accounted for in the analysis. Additionally, the outlier detection would identify candidates for sensitivity analysis in an objective manner. Instead of determining data points that are influential on the results and trying to determine if those points could be considered outliers, we are advocating the converse.

The outlier detection procedures outlined here inherently assume symmetry in the response surface. Thus, it is expected that the trimmed LS technique will provide results similar to those coming from bias correction procedures used in bootstrapping methods (e.g. Prager, 1994). Both methods assume that the underlying distributions are symmetrical and

adjust the results in order to maintain that symmetry. However, if model constraints or other features of the model or data force the response surface to have an underlying (but unknown) skewed distribution, then the outlier selection process outlined here might falsely identify some data points as outliers. Conversely, the least trimmed squares (LTS) solutions make no assumptions about the shape of the response surface. Therefore, we expect that the LTS method could be robust to those situations where the distribution is skewed. Nevertheless, with judicious application, robust regression is expected to be a useful tool for evaluating and selecting data appropriate for tuning stock assessment models.

Acknowledgments

We are grateful to two anonymous reviewers for their critical review of this manuscript. Support for this study was provided through the Cooperative Unit for Fisheries Education and Research (CUFER) by National Oceanic and Atmospheric Administration Cooperative Agreement NA90-RAH-0075.

Literature cited

Barnett, V., and T. Lewis.
1994. Outliers in statistical data, 3rd ed. John Wiley and Sons, New York, NY, 584 p.

Chen, Y., D. A. Jackson, and J. E. Paloheimo.
1994. Robust regression approach to analyzing fisheries data. Can. J. Fish. Aquat. Sci. 51:1420–1429.

Chen, Y., and J. E. Paloheimo.
1994. Robust regression approach to estimating fish mortality rates with a cohort-based model. Trans. Am. Fish. Soc. 123:508–518.

Corana, A., M. Marchesi, C. Martini, and S. Ridella.
1987. Minimizing multimodal functions of continuous variables with the "simulated annealing" algorithm. ACM Trans. Math. Software 13:262–280.

Deriso, R. B., T. J. Quinn II, and P. R. Neal.
1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815–824.

Fournier, D., and C. P. Archibald.
1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. 39:1195–1207.

Hilborn, R.
1990. Estimating the parameters of full age-structured models from catch and abundance data. Bull. Int. N. Pac. Fish. Comm. 50:207–213.

Hilborn, R., and C. J. Walters.
1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York, NY, 570 p.

ICCAT (International Commission for the Conservation of Atlantic Tunas).
1995. Report for the biennial period, 1994–1995, Part I (1994), vol. 2. Int. Comm. Cons. Atl. Tunas, Madrid, Spain, 283 p.

ICES (International Council for the Exploration of the Sea).
1995. Report of the working group on methods of fish stock assessments. Int. Coun. Explor. Sea Coop. Res. Rep. 199, 147 p.

Kimura, D. K.
1989. Variability, tuning, and simulation for the Doubleday-Deriso catch-at-age model. Can. J. Fish. Aquat. Sci. 46:941–949.

Methot, R. D.
1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. Int. N. Pac. Fish. Comm. Bull. 50:259–277.

Nelder, J. E., and R. Mead.
1965. A simplex method for function minimization. The Computer J. 7:308–313.

Pella, J. J., and P. K. Tomlinson.
1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm. (IATTC) Bull. 13:420–496.

Pope, J. G., and J. G. Shepherd.
1985. A comparison of the performance of various methods for tuning VPAs using effort data. J. Cons. Int. Explor. Mer 42:129–151.

Powers, J. E., and V. R. Restrepo.
1992. Additional options for age-sequenced analysis. ICCAT Coll. Vol. Sci. Pap. 39: 540–553.
1993. Evaluation of stock assessment research for Gulf of Mexico king mackerel: benefits and costs to management. N. Am. J. Fish. Manage. 13:15–26.

Prager, M. H.
1994. A suite of extensions to a nonequilibrium surplus-production model. Fish. Bull. 92: 374–389.

Punt, A. E.
1994. Assessments of the stocks of Cape hakes *Merluccius* spp. off South Africa. S. Afr. J. Mar. Sci. 14:159–186.

Restrepo, V. R., and J. E. Powers.
1995. Useful methods for dealing with outliers in stock assessments. Int. Comm. Cons. Atl. Tunas, Coll. Vol. Sci. Pap. Vol. XLIV:151–154.

Restrepo, V. R., J. M. Hoenig, J. E. Powers, J.W. Baird, and S. C. Turner,
1992. A simple simulation approach to risk and cost analysis, with applications to swordfish and cod fisheries. Fish. Bull. 90:736–748.

Rousseeuw, P. J.
1984. Least median of squares regression. J. Am. Stat. Assoc. 79:871–880.

Rousseeuw, P. J., and A. M. Leroy
1987. Robust regression and outlier detection. John Wiley and Sons, New York, NY, 329 p.

Sinclair, A., D. Gascon, R. O'Boyle, D. Rivard, and S. Gavaris
1990. Consistency of some Northwest Atlantic groundfish stock assessments. North Atlantic Fisheries Organization (NAFO) Sci. Council Study 16:59–77.

Steele, J. M., and W. L. Steiger
1986. Algorithms and complexity for least median of squares regression. Discr. Appl. Math. 14:93–100.

Stromberg, A. J.
1993. Computation of high breakdown nonlinear regression parameters. J. Am. Stat. Assoc. 88:237–244.

Growth and survival of 0+ English sole, *Pleuronectes vetulus*, in estuaries and adjacent nearshore waters off Washington

Yunbing Shi*
Donald R. Gunderson
School of Fisheries, 357980, University of Washington
Seattle, Washington 98195
E-mail address: yshi@HARZA.com

Patrick J. Sullivan
International Pacific Halibut Commission
P.O. Box 95009, Seattle, Washington 98145

Abstract.—Growth and mortality rates of 0+ English sole were estimated from field data collected from estuarine and nearshore nursery areas off Washington during 1985–88. Growth of 0+ English sole was approximately linear over time and was estimated with the length modal progression method. Point estimates of growth rates during May through September were in the range of 0.33 to 0.49 mm/day. Statistical analysis with a general linear model showed significant year and settlement time effects on growth of 0+ English sole but failed to detect any density or temperature effect. Instantaneous mortality rate varied significantly with season, declining from 0.0175 per day in July and August to 0.0075 per day in September. Changes in population density appeared to play a minor role in causing this decline.

Fish growth depends on numerous factors, e.g. supply of suitable prey items, ambient temperatures, and oxygen concentration. Laboratory studies have shown that growth of juvenile plaice (*Pleuronectes platessa*), sole (*Solea solea*), and English sole (*Pleuronectes vetulus*) depends strongly on ambient temperature (Williams and Caldwell, 1978; Fonds, 1979; Yoklavich, 1981).

Field observations also show that growth of flatfishes is regulated by ambient temperature. Applying a model based on Fonds's (1979) laboratory experiment and observed temperature data for predicting monthly growth of North Sea plaice, van der Veer et al. (1990) showed a close overall agreement between predicted growth increments and those observed in the field. Simulated growth rates, however, were consistently lower than field-observed growth rates in June, and this tendency was reversed in August (Fig. 7 in van der Veer et al., 1990). This finding suggests that in addition to temperature there are other factors that also affect the growth of plaice.

Laboratory studies of juvenile English sole (Williams and Caldwell, 1978; Yoklavich, 1981) have shown that food limitation can significantly reduce growth. Edwards and Steele (1968) suggested that food limitation was the controlling factor for the growth of North Sea plaice in Loch Ewe. Bergman et al. (1988) reported that growth reduction of 0-group plaice occurred in specific areas of the Wadden Sea where there was low food abundance, although this phenomenon was restricted to only a small part of the population.

Isolating the effects of fish density, food supply, and ambient temperature on growth is difficult with field data. Within a certain range of population density or food abundance, growth may be regulated primarily by temperature and, within a certain range of temperature, population density may have a dominant influence.

Survival is the key element in determining success of recruitment. Early research was largely focused on the "critical period" theory (Hjort, 1913), i.e. survival of small first-feeding larvae is critical to subsequent year-class strength. More recent studies have shown that low

Manuscript accepted 30 July 1996.
Fishery Bulletin 95:161–173 (1997).

* Present address: HARZA Consulting Engineers and Scientists, 2353 130th Avenue N.E., Suite 200, Bellevue, WA 98005.

larval abundance may indicate poor year-class strength, but high larval abundance will not guarantee a strong year class (Bailey and Spring, 1992; Bradford, 1992). Survival during the juvenile stage is critical to year-class success. On the basis of simulation, Bradford (1992) concluded that correlation between recruitment and abundance at early life stages increases monotonically with age, especially during the first 100 days of life, because variation in survival weakens the relationship between recruitment and abundance of early life stages. Although monthly or annual instantaneous mortality is usually higher during the larval stage than that at the juvenile stage, the cumulative mortality might be higher, and more variable, during the juvenile stage because it usually lasts much longer. Therefore any variation in mortality at this stage would induce much greater variation in recruitment.

English sole spawn in offshore areas. Timing of spawning is variable and duration of the spawning period is protracted (August to May, Shi, 1994). The egg and larval stages last from two to two-and-a-half months, and survival and transport of eggs and larvae are dependent on oceanographic conditions (Boehlert and Mundy, 1987, 1988; Shi, 1994). Once metamorphosis and benthic settlement have occurred, English sole actively seek out estuarine nursery areas, and oceanographic influence becomes less important. Analyses of tagging data, distribution of adults, available spawning habitat, and egg distribution (Shi, 1994) suggest that the Grays Harbor and Willapa Bay estuaries serve as nursery areas for English sole that spawn as far south as central Oregon.

This study summarizes results from a series of trawl surveys of Grays Harbor, Willapa Bay, and the adjacent nearshore, 1985–88. Previous work (Gunderson et al., 1990; Shi et al., 1995) has shown that these estuaries provide critical nursery habitat for juvenile English sole during their first year of life.

The abundance of 0+ English sole in our study area (Fig. 1) was relatively stable during September, showing only a threefold difference during 1985–88, despite great variation in settlement in May (Shi et al., 1995). If survival is density dependent, then density could function to stabilize recruitment. In this paper, growth and survival rates will be estimated by using data from field surveys, and we will investigate statistically the effects of population size and ambient temperature on the growth and survival of juvenile English sole.

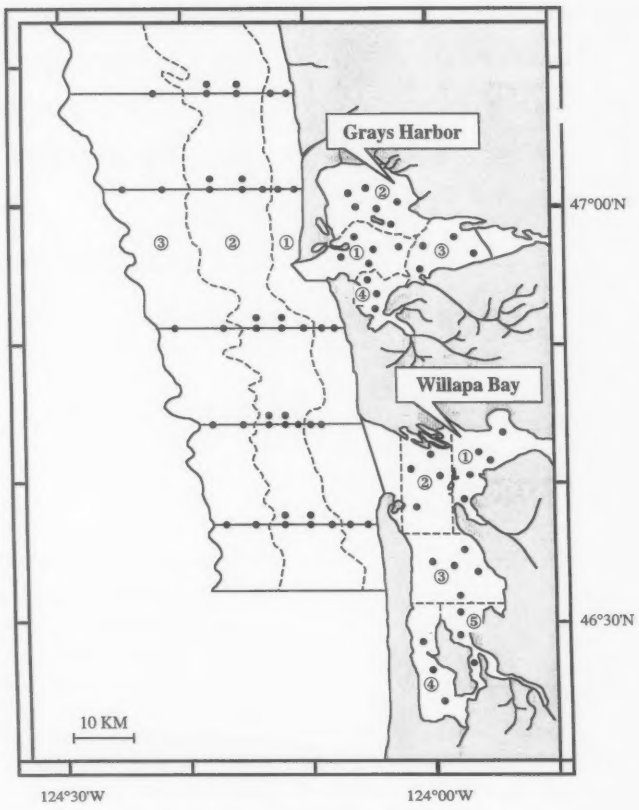


Figure 1

The study area along the southern Washington coast. Shown are subsystem boundaries, nearshore transect lines, trawl stations (filled circles), and stratum numbers (open circles). Dashed lines indicate survey stratum boundaries.

Methods

Study area and field methods

Grays Harbor (8,545 ha) and Willapa Bay (11,200 ha) are two major Washington coastal estuaries characterized by numerous channels, sandflats, and eelgrass beds that provide excellent habitat for 0+ English sole. The nearshore portion of the study area is bounded to the north at 47°15'N, and to the south at about 46°30'N, and extends from the shoreline seaward to 60 m. It encompasses an area of nearly 146,600 ha.

A stratified random trawl survey was performed to estimate population sizes for English sole in both estuaries (Fig. 1) with the area-swept method: $P = A\bar{d}$, where P = population size, A = area of survey stratum (ha), and $\bar{d}$ = mean density (no. of fish caught/

ha) (Shi et al., 1995). Within each stratum, stations were randomly selected from sampling units superimposed on nautical charts, with the constraint that no two stations were immediately adjacent to one another. The effort (number of stations) allocated to each stratum was proportional to the abundance of English sole in that stratum (Shi et al., 1995).

The nearshore area was sampled along fixed transects oriented east–west and trawl stations were located at discrete depths (Fig. 1). Five transects were established, and sampling stations were located at depths of 5, 9, 18, 27, 36, 46, and 55 m. The 55-m station was not sampled on the northernmost transect because of frequent gear damage at this location. Additional effort was allocated to the intermediate stratum; two trawl samples were taken at all 27- and 36-m depths. Sampling stations were stratified according to depth to obtain population estimates. The outer boundary for the nearshore study area was the 59-m (32.5-fm) isobath, and the mean low low water (MLLW) mark was the inner boundary. The boundary separating the inner and middle strata followed the 14-m (7.5-fm) isobath, whereas the boundary between the middle and outer strata was located at 41 m (22.5 fm). The northern and southern limits of the survey area were positioned 5 km beyond the northernmost and southernmost transects.

Each of the three areas was visited once a month. Sampling in estuaries was planned during low spring tides of the month (April or May through September) so that we could navigate among unmarked channels, which otherwise are difficult to see. Stations in close proximity to intertidal areas were sampled preferentially at low tide to minimize bias associated with fish movement onto the tideflats at higher stages of tide. More exposed sites were typically sampled at high water. Trawling operations ceased when tidal currents were judged sufficiently strong that the trawl gear would not tend the ocean bottom properly. Nearshore sampling trips were usually made between the two estuary trips in that month.

Survey samples throughout the study area were collected with a 3-m beam trawl specifically developed for this study (Gunderson and Ellis, 1986). Effective width of the net was 2.3 m, whereas the estimated vertical opening was 0.6 m. The body of the net was composed of 7–9 mm (lumen) knotless nylon, and the codend was lined with 4-mm stretch mesh. A double tickler chain array was attached to a 9.5-kg wingtip weight at each corner of the net. The tickler chain array, together with the turbulent zone it creates, dislodges small animals from the substrate, thus promoting capture by the net.

Nearshore sampling was conducted from the 17-m stern trawler F/V *Karelia*. Tows in the nearshore were taken parallel to isobaths. Scope was routinely 5:1, except at the 5 and 9 m stations where it was 8:1 and 9:1, respectively. Time on the ocean bottom was estimated by using a trigonometric relationship between water depth and wire out, whereas the linear distance towed (mean: 750 m) was determined from LORAN-C readings. Tow duration was routinely 20 minutes at a mean towing speed of 2.6 km/hr (1.4 knots), except at the 5- and 9-m stations, which often yielded excessive quantities of sand dollars (*Dendraster excentricus*) and gravel; tows in these areas were limited to 5 or 10 minutes.

A 6.4-m Boston whaler with a 150-hp outboard engine was used for estuarine trawling. Buoys were deployed at the points where the net first contacted the bottom and subsequently left bottom upon retrieval. The distance towed (mean: 260 m) was estimated with an optical rangefinder. Mean towing speed was 2.8 km/hr (1.5 knots), comparable to that used in the nearshore area.

Data analysis

Length Growth rate estimates were obtained by regressing the mean length of a recruitment influx (indicated by a mode in the length-frequency distribution [Shi et al., 1995]) against the time when samples were taken. There was a linear relationship between modal length and time, as was the case in previous growth studies on juvenile English sole (Ketchen, 1956; Kendall, 1966; Rosenberg, 1982). Because size-dependent migration between nearshore and estuarine systems occurs, with smallest juveniles migrating into estuaries and larger fish moving offshore (Gunderson et al., 1990; Shi et al., 1995), separate estimates of growth rates for nearshore and estuarine fish would be inappropriate. To minimize the effect of interregional migrations, the mean lengths at each mode (defined on the basis of visual inspection of monthly length frequency plots [Shi et al., 1995]) were calculated from the estimated size composition of the overall population. The length statistic used was the mean modal length (MML), which is defined as the mean length within a mode, weighted by the estimated population size for each size group:

$$MML = \frac{\sum_{l=l_{low}}^{l_{up}} l\hat{P}_l}{\sum_{l=l_{low}}^{l_{up}} \hat{P}_l}, \quad (1)$$

where, $\hat{P}_l$ = estimated population (millions) of fish in length group l; l_{up} and l_{low} = length (mm) at upper and lower limits of the mode, which are so defined that l_{up} and l_{low} are the length groups at which abundance has declined to half that at the modal size (Fig. 2). If length is normally distributed, $l \sim N(\bar{l}, s^2)$, the population within the upper and lower limits of the mode so defined would account for about 75% of the total population of that cohort (Shi, 1994).

Date The dates used in growth and mortality estimation were also population-weighted means. The dates when the samples were taken cannot be used directly in growth and mortality estimation without being standardized. Estuarine samples had to be taken during low low tide (LLT) periods, and we were often forced to take estuarine samples at unequal time intervals.

We made every effort to carry out the monthly nearshore surveys during the intervals between the Grays Harbor and Willapa Bay surveys, but they sometimes had to be done either before or after the estuarine trips owing to logistic difficulties. This made the time between the first and last surveys for a given month more than a half-month apart. The population-weighted mean date (PWMD) was chosen to standardize the "date" of monthly surveys and is the best estimate of the average sampling date for the total population in our study area. The PWMD was computed from

$$PWMD_{jm} = \frac{\sum_{i=1}^{3} P_{ijm}\,\overline{date}_{ij}}{\sum_{i=1}^{3} P_{ijm}}, \qquad (2)$$

where, $PWMD_{jm}$ = population-weighted mean date in month j (May, June, July, August, and September) for mode m (1 or 2); P_{ijm} = population of mode m in system i (GH, WB, NS), month j; $\overline{date}_{ij}$ = mean date of a survey carried out in month j and system i, i.e. number of days from 1 May.

Temperature A population-weighted mean bottom temperature (PWMBT) was developed in this study because of extensive seasonal ontogenetic migrations

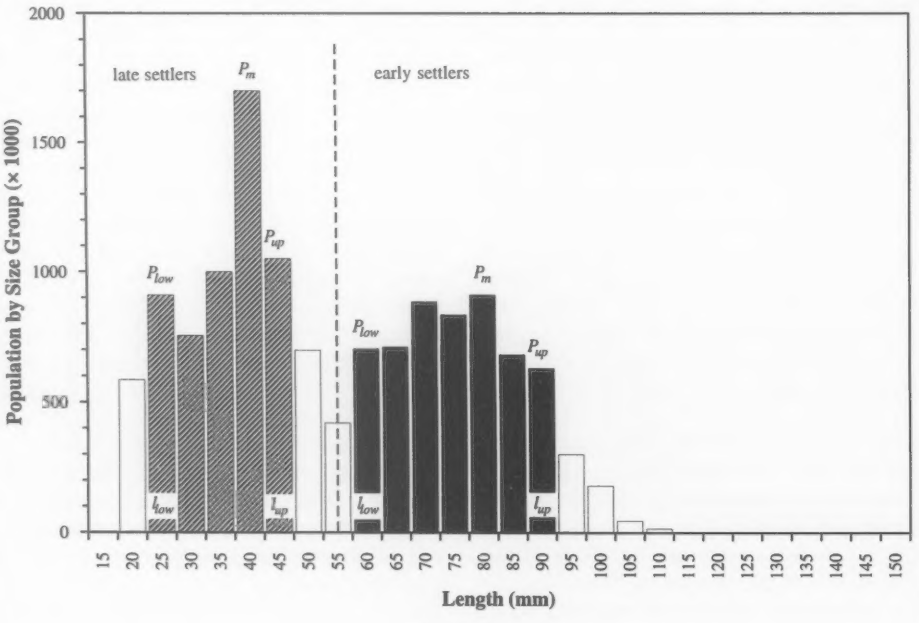


Figure 2

A diagram illustrating how the upper (l_{up}) and lower (l_{low}) limits of a mode were determined. P_m is the estimated modal population and P_{low}, P_{up} are the estimated population of the lower and upper limits of the mode.

between estuarine and nearshore areas and because of differences in mean bottom temperatures between estuarine and nearshore systems (2–8°C, Fig. 3).

$$PWMBT_{jm} = \frac{\sum_{i=1}^{3}\sum_{s=1}^{s_i} P_{isjm}\overline{T}_{isj}}{\sum_{i=1}^{3}\sum_{s=1}^{s_i} P_{isjm}}, \qquad (3)$$

where, $PWMBT_{jm}$ = population-weighted mean bottom temperature in month j for mode m; P_{isjm} = population of mode m in system i, stratum s, month j; $\overline{T}_{isj}$ = mean bottom temperature in system i, stratum s, and month j; and s_i = number of strata in system i. $PWMBT_{jm}$ is the best estimate of the average temperature experienced by the population in our study area.

Growth rates A linear model was developed to determine competing factors that had significant effects on the growth of 0+ English sole.

$$l_{ji} = \alpha + \alpha_1 c + \alpha_{2j} y_j + \beta t_i + \beta_1 c t_i + \beta_{2j} y_j t_i + \beta_3 d_i t_i + \beta_4 T_i t_i + \varepsilon_{ji}, \qquad (4)$$

where, l_{ji} = mean modal length (MML) at time t_i and year j; y_j and c are dummy variables for year and settlement time; t_i = population weighted mean date (PWMD); d_i = density (no/ha), monthly mean density from May through September; T_i = population weighted mean bottom temperature ($PWMBT$); and ε_{ji} = residual. The d_i and T_i terms were used to examine whether or not there were density or temperature effects (or both) on the growth of 0+ English sole in the study areas. The dummy variable y_j (year) was defined as follows:

$$y_1 = \begin{cases} 1 & 1986 \\ 0 & \text{otherwise} \end{cases}, \quad y_2 = \begin{cases} 1 & 1987 \\ 0 & \text{otherwise} \end{cases},$$

$$y_3 = \begin{cases} 1 & 1988 \\ 0 & \text{otherwise} \end{cases}.$$

Since, settlement time obviously differed between cohorts (Fig. 4), the dummy variable (c) was used to denote early (1) and the late (0) settlement groups:

$$c = \begin{cases} 1 & \text{early settlements (1985, 1986 – 1, 1988)} \\ 0 & \text{late settlements (1986 – 2, 1987).} \end{cases}$$

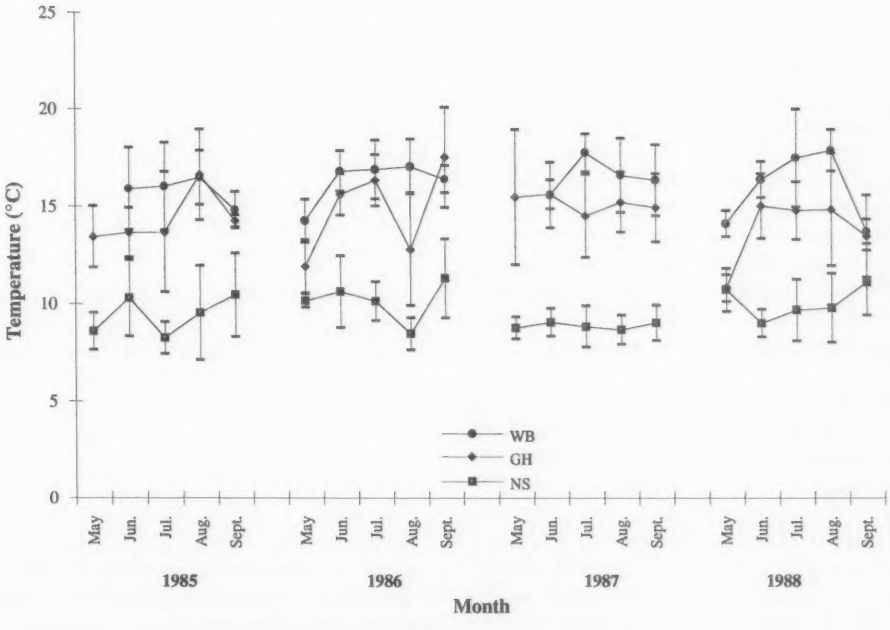


Figure 3

Monthly unweighted mean bottom temperature (°C) by area from years 1985 to 1988. Bars indicate one standard deviation. WB = Willapa Bay; GH = Grays Harbor; NS = nearshore.

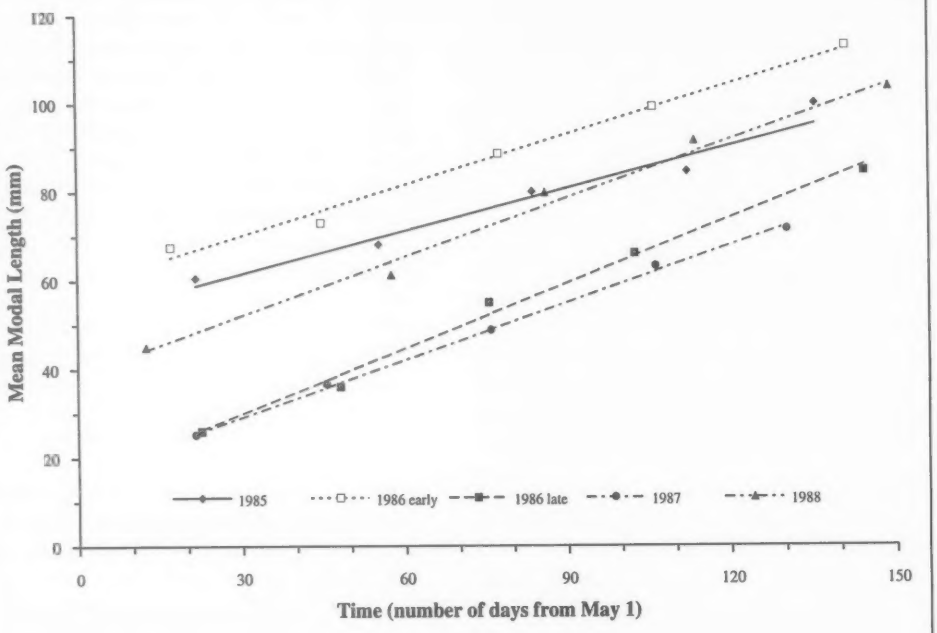


Figure 4

A plot of mean modal length (MML, mm) against population-weighted mean date (PWMD) to illustrate the growth trajectory of 0+ English sole, May through September, 1985–1988.

Early and late settlement was defined by visual inspection of length frequency (Shi et al., 1995). A recruitment influx with mean modal length less than 40 mm during the May survey was defined as late settlement, and that with mean modal length greater than 40 mm in May was defined as early settlement. A multiple-partial F-test was used here to test the significance of settlement time ($\beta_1 c$), year ($\beta_{2j} y_j$), density ($\beta_3 d_i$), and temperature ($\beta_4 T_i$) effects on growth. The computer program MGLH (SYSTAT [Wilkinson, 1989]) was used to carry out all calculations.

Mortality rates The significance of density and season effects on mortality was examined by using the restated Beverton-Holt equation (Beverton and Iles, 1992):

$$\frac{dP}{Pdt} = -(\mu_1 + \mu_2 \ln P), \tag{5}$$

where P is the population of juvenile English sole in our study area; μ_1 is the density independent coefficient, as defined in Beverton and Iles (1992), and μ_2 is the density-dependent coefficient.

Population estimates from the surveys were fitted to the following three competing models, by using nonlinear least-squares regression (Wilkinson, 1989):

1) By integrating Equation 5 with $\mu_2 = 0$, the density-independent mortality model is

$$P_{t_i} = P_{oi} e^{-\mu_1 t_i}. \tag{6}$$

2) Integrating Equation 5 over the time period from $t = 0$ to $t = t_i$ without any constraint on μ_1 or μ_2, the full model is

$$P_{t_i} = e^{\frac{\mu_1}{\mu_2}(e^{-\mu_2 t_i} - 1)} P_{oi}^{e^{-\mu_2 t_i}}. \tag{7}$$

3) Integrating Equation 5 with $\mu_2 = 0$, and allowing μ_1 to vary, the model becomes

$$P_{t_i} = \begin{cases} P_{oi} e^{-\mu' t_i} & t_i = 0 \text{ to } 31 \text{ (July)} \\ P_{oi} e^{-\mu'(32)} e^{-\mu''(t_i - 32)} & t_i = 32 \text{ to } 62 \text{ (August)} \\ P_{oi} e^{-\mu'(32)} e^{-\mu''(62-32)} e^{-\mu'''(t_i - 62)} & t_i > 62 \text{ (September)} \end{cases} \tag{8}$$

where t_i = time, number of days elapsed since 1 July for surveys conducted in year i (1985–88); P_{t_i} = the observed total population size (0+ group) for all areas combined at time t_i in year i; and P_{oi} = initial total population size on 1 July in year i. P_{oi} was estimated as a parameter along with the coefficients μ_1 and μ_2. μ', μ'', and μ''' are the density-independent mortality

Table 1

Monthly population-weighted mean date (PWMD), mean modal length (MML), population-weighted mean bottom temperature (PWMBT) and overall mean densities of 0+ English sole, 1985–88.

Year	Settlement time	Month	PWMD (days)	MML (mm)	PWMBT (°C)	Density[1] (No./ha)
1985	Early	May	21.66	60.56	13.07	55.03
		Jun	55.34	68.08	14.66	130.95
		Jul	83.75	79.95	12.94	200.60
		Aug	112.39	84.55	14.34	132.69
		Sep	135.72	99.96	12.24	96.42
1986	Early	May	17.05	67.54	13.61	118.25
		Jun	44.71	72.97	16.24	77.06
		Jul	77.54	88.58	14.66	96.75
		Aug	106.18	99.17	12.07	72.55
		Sep	141.32	112.98	12.49	65.80
1986	Late	May	22.51	25.99	12.33	118.25
		Jun	48.11	36.09	15.31	77.06
		Jul	75.63	55.01	15.43	96.75
		Aug	102.64	66.10	14.63	72.55
		Sep	144.51	84.67	14.81	65.80
1987	Late	May	21.47	25.17	10.48	188.77
		Jun	45.58	36.64	13.70	219.35
		Jul	76.00	48.83	15.28	346.38
		Aug	106.47	63.19	12.48	186.98
		Sep	130.45	71.49	13.65	200.48
1988	Early	May	12.48	45.01	13.21	269.44
		Jun	57.61	61.24	15.20	193.18
		Jul	86.10	79.77	14.91	182.15
		Aug	113.75	91.58	14.78	116.13
		Sep	149.10	103.72	12.26	90.31

[1] The estimated densities are combined densities of early and late recruits.

coefficients during July, August, and September, respectively. Model selection was based on the Bayesian Information Criterion (BIC) proposed by Schwarz (1976).

Results

The mean modal length (MML), population-weighted mean date (PWMD), population-weighted mean bottom temperature (PWMBT), and overall mean densities of 0+ English sole from May through September are shown in Table 1.

Growth

Growth of 0+ English sole was linear over time (Fig. 4). A general linear model pooled all data together and considered the effects of year, time of settlement, density, and temperature on growth. The final, best-fitted ($R^2 = 0.99$, $P < 0.001$) model was

$$l_{ji} = 8.44 + 43.48c + 6.76y_1 + 7.79y_2 - 13.06y_3 + 0.43t_i - 0.11ct_i + 0.06y_1t_i + 0.12y_3t_i + \varepsilon_{ji}.$$

The results of partial t-tests (used in all comparisons unless specified otherwise), indicated there was a significant settlement time effect on growth ($P<0.01$), late-settling cohorts growing the fastest. The year effect was also significant (multiple partial F-test $P<0.05$, Table 2). Multiple-partial F-tests indicated that there were no density ($P=0.80$) or temperature ($P=0.37$) effects on the growth of 0+ English sole.

The date of settlement was estimated by fitting separate regression equations to each cohort in Figure 4, then by backcalculating to a length of 20 mm TL (Table 3), or by inverse prediction (Neter et al., 1985). We estimated that settlement of the 1985 and 1986 group-1 cohorts peaked in January, with 95% prediction intervals ranging from 27 November to 22 March. Settlement of the 1986 group-2 and 1987 cohorts peaked in May (with 95% prediction intervals ranging from 21 April to 29 May), and that of the 1988 cohort peaked in March (ranging from 17 February to 16 April).

Mortality The following equations were obtained from nonlinear least-square regression:

Table 2

A summary of effects of year and settlement time on the growth of 0+ English sole.

	Variable	Parameter	Coefficient	Partial-t	P (2-tail)
Intercept	Constant	α	8.44	3.19	< 0.01
	Settlement Time (c)	α_1	43.48	17.03	< 0.01
	Year (y_1, y_2, y_3)	—	—	—	< 0.01[1]
	y_1	α_{21}	6.76	2.61	< 0.05
	y_2	α_{22}	7.79	3.58	< 0.01
	y_3	α_{23}	–13.06	–4.19	< 0.01
Slope (Growth)	PWMD (t_i)	β	0.43	18.45	< 0.01
	Settlement time (c)	β_1	–0.11	–4.04	< 0.01
	Year (y_1, y_2, y_3)	—	—	—	< 0.05[2]
	y_1	β_{21}	0.06	2.13	< 0.05
	y_3	β_{23}	0.12	3.66	< 0.01

[1] Based on the result of an F-test, $F_{3,15} = 4.35$.
[2] Based on the result of an F-test, $F_{3,15} = 13.25$.

$$\text{Model 1}: \mu_2 = 0,\ P_{t_i} = P_{oi}e^{-0.0123t_i};\qquad P_{oi} = \begin{cases} 42.82 & 1985 \\ 21.02 & 1986 \\ 66.63 & 1987 \\ 40.40 & 1988 \end{cases}$$

$$\text{Model 2}: P_{t_i} = e^{\frac{-0.0066}{0.0056}\left(e^{-0.0056t_i}-1\right)}P_{oi}^{e^{-0.0056t_i}};\ P_{oi} = \begin{cases} 43.80 & 1985 \\ 18.62 & 1986 \\ 73.33 & 1987 \\ 40.46 & 1988 \end{cases}$$

$$\text{Model 3}: P_{t_i} = \begin{cases} P_{oi}e^{-0.0175t_i} \\ P_{oi}e^{-0.0175\times 62}e^{-0.0075(t_i-62)}. \end{cases}$$

$t_i = 0$ to 62 (July and August)

$t_i > 62$ (September)

$$P_{oi} = \begin{cases} 49.60 & 1985 \\ 23.23 & 1986 \\ 74.33 & 1987 \\ 47.28 & 1988 \end{cases}$$

The estimated instantaneous mortality rates of 0+ English sole in July and August were equal, therefore model 3 was reduced from a three-step to a two-step model. The data fitted model 3 best (Fig. 5) with instantaneous mortality rates of 0.0175 per day in July and August and 0.0075 per day in September. The value of the Bayesian information criterion was 3.68 for model 1, 4.04 for model 2, and 2.65 for model 3. As a result, we concluded that model 3 was the best for estimating mortality.

Table 3

Back-calculated settlement dates with their ranges, assuming average length at settling, $l_{settling}$ = 20 mm TL.

Year	Settlement cohort	Date of settlement	95% prediction interval
1985	1	24 Jan	27 Nov–22 Mar
1986	1	16 Jan	17 Dec–16 Feb
	2	10 May	21 Apr–29 May
1987	2	8 May	30 Apr–16 May
1988	1	18 Mar	17 Feb–16 Apr

Discussion

Gear efficiency

Our estimates of growth and mortality might be biased if gear selectivity varied with size. Edwards and Steele (1968) suggested that beam trawl efficiency depends on a number of factors, such as towing speed, bottom type, and fish size. At a speed of 35 m/min, the efficiency of their 2-meter beam trawl was 25–35%, depending on fish size. They point out that their results apply only to their particular gear and the special conditions in Loch Ewe. Kuipers (1975) found that the efficiency of a 2-m beam trawl in the Dutch Wadden Sea declined from 100% at lengths below 70 mm to 15–30% for plaice larger than 150 mm. Our gear was a 3-m beam trawl with effective fishing width of 2.3 m, wider than the gear used by either Kuipers or Edwards and Steele, and was towed faster (41–47 m/min vs. 30–35 m/min). Also the ratio of fish-

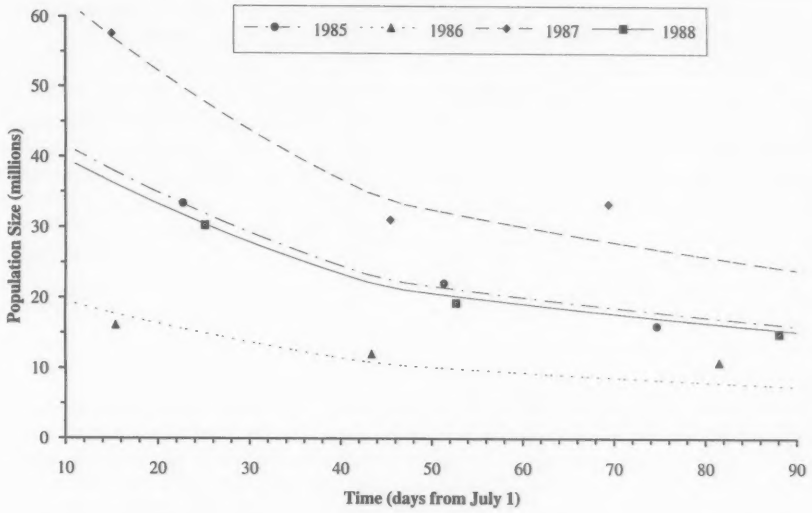


Figure 5

Population sizes (millions) plotted against time (number of days from 1 July) for 0+ English sole off Washington during July through September, 1985–88. All lines represent the predicted trajectories with the month-specific, density independent mortality model (model 3); solid symbols represent the observed data.

ing line out to bottom depth used in our survey (10–15 in shallow waters) was greater than that in Kuipers' experiment (4–8), resulting in better bottom contact and reduced vessel avoidance.

During a series of 15 pairs of day–night comparative tows, for which gear and operating procedures were the same as those described in this paper, Gunderson and Ellis (1986) failed to detect any significant net avoidance by either butter sole (*Pleuronectes isolepis)* over the length range from 40 to 280 mm, or Pacific tomcod (*Microgadus proximus)* over the length range from 60 to 220 mm. In the present study, the data for English sole did not show any decline in estimated growth with size (Fig. 4). We conclude that the efficiency of the gear used in this study does not decrease with fish size over the length range from 20 to 150 mm and has little influence on estimates of growth or mortality.

Growth

It has been shown that English sole juvenile migration in and out of estuaries is size dependent (Gunderson et al., 1990; Shi et al., 1995), and our approach to the length modal progression method (LMP), namely pooling length data from coastal and estuarine areas to estimate growth, accounts for the effect of such migrations. Our nearshore survey area covered the outer limit of 0+ English sole bathymetric distribution; less than 1% of the total population was found in the deepest nearshore stratum (Shi et al., 1995). To minimize the effects of inter-area migration, we pooled data from all three areas surveyed (Fig. 1), which cover a major portion of waters available to English sole juveniles along the Washington coast. The resulting estimates fall between faster growth rates estimated from previous LMP analyses (Westrheim, 1955; Smith and Nitsos, 1969; Krygier and Pearcy, 1986) and slower growth rates estimated from fortnightly ring counts by Rosenberg (1982) (Table 4). Gunderson et al. (1990) and Shi et al. (1995) suggested that the population of English sole juveniles in this study may not be closed, however, and that some migrations, especially during May and June each year, involve areas outside the study area shown in Figure 1. Continuous recruitment of young juveniles from outside the study area would result in an underestimation of growth rates, as could emigration of larger juveniles. Our data do not show any decline in growth at either the beginning or end of the survey season (Fig. 4); thus the influence of continuous recruitment of small fish or emigration of larger fish on growth estimation appeared to be minimal.

Table 4

A summary of daily growth rate estimates from field studies.

Location	Size at age 1-yr (mm TL)	Daily growth rate (mm/day)	Data source
Willapa Bay, Grays Harbor, and adjacent neashore, WA	≤150	0.33–0.49 (May–Sep)	This study, 1985–88
Yaquina Bay, OR	130–160	0.49 (May–Oct)	Westrheim, 1955
Monterey Bay, CA	130–150	0.55 (May–Oct)	Smith and Nitsos, 1969
Yaquina Bay, OR	100–140	0.33	Rosenberg, 1982[1,2]
Moolach Beach, OR	100	0.34	
Yaquina Bay, OR	≤150	0.46–0.49 (Mar–Oct) 0.26–0.32 (Dec–Apr)	Krygier and Pearcy, 1986[2]
Moolach Beach, OR	≤150	0.28–0.42 (Apr–Oct)	

[1] The original daily growth rates were estimated from fortnightly ring counts.
[2] Length at age 1 and daily growth rates were converted from standard length (SL) to total length (TL) by using the relationship: $SL = -0.205 + 0.848\ TL$ (senior author, unpubl. data).

Several previous studies with the LMP technique have attempted to estimate growth rates for English sole juveniles from estuaries and open coast but failed to consider the effect of interarea migration on the growth estimates. As a consequence, their results often show significant differences between coastal and estuarine populations (Westrheim, 1955; Smith and Nitsos, 1969; Krygier and Pearcy, 1986). In contrast, growth estimated from fortnightly ring counts showed no differences between coastal and estuarine populations (Rosenberg, 1982).

Previous laboratory studies where ration was held constant (Williams and Caldwell, 1978) showed that ambient temperature had no statistically significant effect on English sole growth rate between 9.5 and 15.0°C but significantly reduced growth between 15.0 and 18.0°C. The artificial food pellets used in that study may have been nutritionally inadequate, however, making it difficult to extrapolate the results to field conditions. Laboratory studies by Yoklavich (1981), where live polychaetes were used as food, showed a significant decline in the mean growth rate of 0⁺ English sole (from 1.87% to 1.17% of body weight per day) between 13.0 and 17.5°C. Our results do not indicate any statistically significant interannual effect of temperature on the growth of English sole juveniles over the range of population-weighted mean temperatures (10.5–16.2°C) observed under field conditions. Higher temperatures presumably result in increased benthic productivity (Johnson and Brinkhurst, 1971) and in more food available to juveniles. On the other hand, metabolic requirements increase at high temperatures. Whether the juveniles grow faster or slower under field conditions probably depends on the bioenergetic balance at higher temperatures.

Peterman and Bradford (1987) found that density had a significantly negative effect on the growth of 1⁺ English sole off the Oregon and Washington coasts (P=0.024, one-tailed t-test); therefore it would be reasonable to expect that growth of 0⁺ English sole is also density dependent. Nevertheless growth rate and mean population size varied over relatively narrow ranges in this study, and we were unable to detect any statistically significant density effect.

The spawning season for English sole can extend from September to April (Kruse and Tyler, 1983), and recruitment processes are also protracted. Multiple peak recruitments are common (Kendall, 1966; Boehlert and Mundy, 1987; Gunderson et al., 1990; Shi et al., 1995), and peak recruitment occurs at different times each year, depending on ocean temperature and transport mechanisms (Ketchen, 1956; Boehlert and Mundy, 1987). Kendall (1966) reported that for Puget Sound English sole juveniles that were recruited earlier, growth was slower than that of later recruits during the same period. Our results led to the same conclusion, that is, timing of settlement influences the growth trajectory (Fig. 4).

Different size groups of English sole have different prey requirements and suffer from different degrees of food limitation (Gunderson et al., 1990). Off the Oregon coast, English sole 17–35 mm standard length (SL) fed primarily on polychaete palps, juvenile bivalves, and harpacticoid copepods, whereas 35–82 mm fish fed on larger prey such as amphipods and cumaceans (Hogue and Carey, 1982). In the Humboldt Bay estuary, English sole smaller than 50 mm TL fed almost exclusively on harpacticoid copepods whereas the diet of 66–102 mm fish was dominated by polychaetes (Toole, 1980).

Winberg (1956) found that individual metabolic requirements and food consumption increase as a function of $W^{0.8}$ (where W=body weight), and Fonds (1979) showed a similar relation for young sole, *Solea solea*. The larger sizes attained by the early-settlement cohorts of English sole would probably also entail increased food requirements for those fish during May–September. The lower growth rates observed for early-settlement cohorts in comparison with those that settled later probably resulted from a combination of higher metabolic demands and reduced availability of suitable prey. Growth of 0+ English sole does not appear to be strictly linear if a sufficiently long period of time is examined.

Mortality

Estimates of mortality rates were subject to some of the same sources of error and bias that the growth estimates were. Previous work (Gunderson et al., 1990; Shi et al., 1995) has shown that migrations of 0+ English sole are size dependent. Typically, larger fish emigrate from estuaries and perhaps out of our nearshore survey area, whereas smaller fish immigrate into our survey area. Immigration of small fish would cause underestimates of mortality. Previous analysis indicated that most immigration probably occurred near the settling period, i.e., May and June or earlier (Shi et al., 1995). Therefore, it is unlikely that immigration had much effect on the mortality estimates because only population estimates for July through September were used in this analysis.

Emigration of large 0+ fish would cause overestimation of mortality rates. Although we cannot completely ignore the possibility of emigration, previous analysis of length increment patterns in estuarine and nearshore areas has indicated that net emigration of large fish from the study area is minor during July–September (Shi et al., 1995). In addition, had substantial emigration occurred during July through September, estimated mortality rates would be consistently higher during September than during July and August, rather than the opposite (0.0075 per day vs. 0.0175 per day).

Seasonally differentiated daily mortality could be related to differences in temperature, individual size, or population density. Water temperatures, however, remained relatively stable in the study area during July through September (Fig. 3). Size-dependent mortality may have occurred, because 0+ English sole grow rapidly during the summer, with increases in individual size of 0+ English sole ranging from 20 to 30 mm TL from July to September. Kramer (1991) estimated the mortality rates for each 5-mm size group of California halibut, *Paralichthys californicus*, on the basis of daily production by size group, and found that mortality was size specific for fish less than 70 days old (< 30 mm SL), smaller fish suffering higher mortality than larger ones. For older 0+ California halibut (70–115 days of age or 31–70 mm SL), mortality varied little (0.011– 0.014 per day, with mean=0.0124 per day and SD=0.001 per day) and no trend was observed. Beverton and Iles (1992) found a significant density-dependent mortality (μ_2) effect for North Sea plaice ranging from ≤15 mm to 35 mm, although this effect was not significant for fish larger than 35 mm. Both Kramer (1991) and Beverton and Iles (1992) found that mortality of juvenile flatfish is highest during and immediately after settlement, and our results for English sole suggest the same.

The effects of density and individual size were clearly confounded in our study (Fig. 6). An empirical relation between population size in the survey area (P_t) and mean length (l_t) was fitted as

$$\ln P_t = A + Bl_t,$$

where, P_t = the estimated total population size at time t; l_t = the mean length of all 0+ English sole at time t (July through September); and the correlation between the two confounding factors was highly significant (r^2=0.56, P<0.01). It should always be borne in mind that it is very difficult, if not impossible, to isolate these two confounding factors in field observations; controlled enclosure experiments would probably be required to disentangle them. There is both a theoretical (Peterson and Wroblewski, 1984) and an empirical (McGurk, 1986; Kramer, 1991) basis for assuming that mortality decreases with individual size, and if this is the case, μ_2 (the density-dependent mortality coefficient) would have been overestimated. If mortality of 0+ English sole is density dependent, it appears that this dependence is weak because adding a density-dependent term to the model (model 2) did not improve the fit to the data.

Our surveys showed only a threefold difference in abundance of 0+ English sole during 1985–88, but stock synthesis analysis of commercial fisheries data indicates this was a period of relatively stable recruitment (Sampson[1]). The estimated recruitment of age-2+ females to the commercial fishery varied by no more than a factor of 1.8 for the 1985–88 year classes, whereas it varied by a factor of 6.5 for the

[1] Sampson, D. B. 1993. An assessment of the English sole stock off Oregon and Washington in 1992. Appendix H *in* Status of the Pacific coast groundfish fishery through 1993 and recommended allowable biological catch for 1994. Pacific Fish. Management Council, 2000 SW 1st Ave., Suite 420, Portland, OR, 43 p.

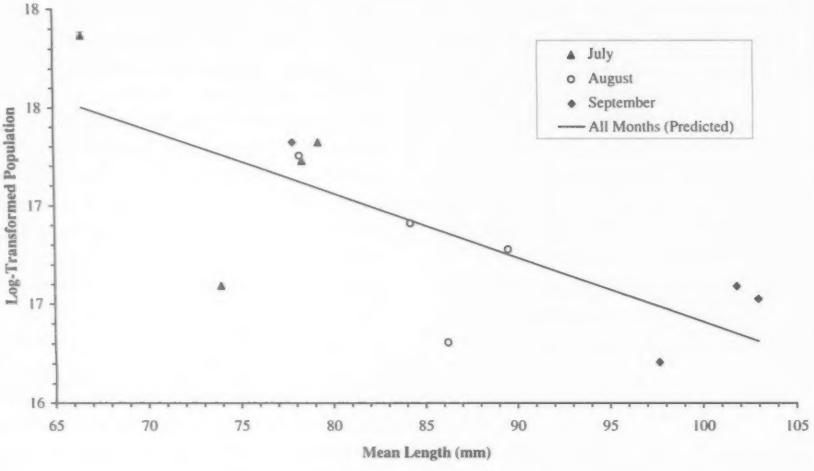


Figure 6

A plot illustrating the correlation (r^2=0.56, P<0.01) between population size and individual size.

1975–90 year classes. Although our results apparently did not encompass periods of poor recruitment, they show that surveys of the nursery areas of 0+ English sole have the potential to provide estimates of year-class strength several years in advance of the commercial fishery, as well as provide insight into the processes that generate recruitment variability.

Acknowledgments

The senior author is grateful to his graduate committee members and fellow graduate students for their support and assistance during this study. This research was supported by grants from Washington Sea grant (NA 86AA-D-SG004) and the National Marine Fisheries Service (NOAA).

Literature cited

Bailey, K. M., and S. M. Spring.
1992. Comparison of larval, age-0 juvenile and age-2 recruit abundance indices of walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska. ICES J. Mar. Sci. 49:297–304.

Bergman, M. J. N., H. W. van der Veer, and J. J. Zijlstra.
1988. Plaice nurseries: effects on recruitment. J. Fish. Biol. 33 (suppl. A):210–218.

Beverton, R. J. H., and T. C. Iles.
1992. Mortality rates of 0-group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus* L.) in European waters. III: Density-dependence of mortality rates in 0-group plaice, and some demographic implications. Neth. J. Sea Res. 29:61–79.

Boehlert, G. W., and B. C. Mundy.
1987. Recruitment dynamics of metamorphosing English sole, *Parophrys vetulus*, to Yaquina Bay, Oregon. Estuarine Coastal Shelf Sci. 25:261–281.
1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Am. Fish. Soc. Symp. 3:51–67.

Bradford, M. J.
1992. Precision of recruitment predictions from early life stages of marine fishes. Fish. Bull. 90:439–453.

Edwards, R., and J. H. Steele.
1968. The ecology of 0-group plaice and common dabs at Loch Ewe. I. Population and food. J. Exp. Mar. Biol. Ecol. 2:215–238.

Fonds, M.
1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. *In* E. Naylor and R. G. Hartnell (eds.), Proceedings of the 13th European marine biology symposium, p.151–156. Pergamon Press, Oxford, 477 p.

Gunderson, D. R., and I. E. Ellis.
1986. Development of a plumb staff beam trawl for sampling demersal fauna. Fish. Res. 4:35–41.

Gunderson, D. R., D. A. Armstrong, Y. B. Shi, and R. A. McConnaughey.
1990. Patterns of estuarine use by juvenile English sole (*Parophrys vetulus*) and Dungeness crab (*Cancer magister*). Estuaries 13:59–71.

Hjort, J.
1913. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 19:1–228.

Hogue, E. W., and A. G. Carey Jr.
1982. Feeding ecology of 0-age flatfishes at a nursery ground on the Oregon Coast. Fish. Bull. 80:555–565.

Johnson, M. G., and R. O. Brinkhurst.
1971. Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28:1699–1714.

Kendall, A. W., Jr.
1966. Sampling juvenile fishes on some sandy beaches of Puget Sound, Washington. M.S. thesis, Univ. Washington, Seattle, WA, 77 p.

Ketchen, K. S.
1956. Factors influencing the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, British Columbia. J. Fish. Res. Board Can. 13(5):647–694.

Kramer, S. H.
1991. Growth, mortality, and movements of juvenile California halibut, *Paralichthys californicus*, in shallow coastal and bay habitats of San Diego County, California. Fish. Bull. 89:195–207.

Kruse, G. H., and A. V. Tyler.
1983. Simulation of temperature and upwelling effects on the English sole (*Parophrys vetulus*) spawning season. Can. J. Fish. Aquat. Sci. 40:230–237.

Krygier, E. E., and W. G. Pearcy.
1986. The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, off Oregon. Fish. Bull. 84:119–132.

Kuipers, B. R.
1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). Neth. J. Sea Res. 9: 69–85.

McGurk, M. D.
1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Mar. Ecol. Prog. Ser. 34:227–242.

Neter, J., W. Wasserman, and M. H. Kutner.
1985. Applied linear statistical models. Regression, analysis of variance and experimental designs, 2nd ed. Irwin, Homewood, IL, 1127 p.

Peterman, R. M., and M. J. Bradford.
1987. Density-dependent growth of age 1 English sole (*Parophrys vetulus*) in Oregon and Washington coastal waters. Can. J. Fish. Aquat. Sci. 44:48–53.

Peterson, I., and J. S. Wroblewski.
1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41:1117–1120.

Rosenberg, A. A.
1982. Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursey grounds. Fish. Bull. 80:245–252.

Schwarz, G.
1976. Estimating the dimension of a model. Ann. Statist. 6:461–464.

Shi, Y.
1994. Recruitment of juvenile English sole, *Pleuronectes vetulus*, in estuaries and nearshore areas of Washington. Ph.D. diss., Univ. Washington, Seattle, WA, 148 p.

Shi, Y., D. R. Gunderson, and D. A. Armstrong.
1995. Population dynamics of 0+ English sole, *Pleuronectes vetulus*, in estuaries and nearshore areas of Washington. *In* Proceedings of the international symposium on North Pacific flatfish, p. 343–365. Alaska Sea Grant College Program Report 95-04, Univ. Alaska, Fairbanks.

Smith, J. G., and R. J. Nitsos.
1969. Age and growth studies of English sole, *Parophrys vetulus*, in Monterey Bay, California. Pac. Mar. Fish Comm. Bull. 7:74–79.

Toole, C. L.
1980. Intertidal recruitment and feeding in relation to optimal utilization of nursery areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). Env. Biol. Fish. 5(4):383–390.

van der Veer, H. W., L. Pihl, and M. J. N. Bergman.
1990. Recruitment mechanism in North Sea plaice, *Pleuronectes platessa*. Mar. Ecol. Prog. Ser. 64:1–12.

Westrheim, S. J.
1955. Size composition, growth, and seasonal abundance of juvenile English sole (*Parophrys vetulus*) in Yaquina Bay. Res. Briefs. Fish Comm. Oregon 6(2):4–9.

Wilkinson, L.
1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL, 822 p.

Williams, S. F., and R. S. Caldwell.
1978. Growth, food conversion and survival of 0-group English sole (*Parophrys vetulus* Girard) at five temperatures and five rations. Aquaculture 15:129–139.

Winberg, G. G.
1956. Rate of metabolism and food requirements of fishes. Nauchye Trudy Belorusskogo Gosudarstvennogo Universiteta Imeni. V. I. Lenina, Minsk, 253 p. (Fish. Res. Board Can. Trans. Ser. 194, 202 p.).

Yoklavich, M.
1981. Growth, food consumption, and conversion efficiency of juvenile English sole (*Parophrys vetulus*). Proceeding of the 3rd Pacific workshop on fish food habits studies, p. 97–105. Washington Sea Grant Rep WSG-WO-82-2.

Mitochondrial DNA diversity in and population structure of red grouper, *Epinephelus morio*, from the Gulf of Mexico*

Linda R. Richardson
John R. Gold
Department of Wildlife and Fisheries Sciences
Texas A&M University
College Station, Texas 77843-2258
E-mail address: lindafish@tamu.edu

Red grouper, *Epinephelus morio*, is a protogynous hermaphrodite found exclusively in the Atlantic Ocean from the coast of Massachusetts southward to Brazil (Smith, 1961). It is most abundant along the western Florida shelf and off the north coast of the Yucatan Peninsula, Mexico (Brulé and Canché, 1993). Studies on the biology of red grouper are few. Adults are known to be associated with rocky reef bottoms and caverns, ledges, and crevices formed by limestone outcroppings (Moe, 1969). Other available data include food habits and some aspects of early life history and patterns of migration (Moe, 1969; Brulé and Canché, 1993).

Red grouper are important to both commercial and recreational fisheries in the United States (U.S.) and Mexico (Moe, 1969). In recent years, declines in recreational and commercial landings have led to regulation of both fisheries in U.S. waters. The Mexican red grouper fishery, reportedly working above maximum sustainable yield (Solís Ramírez, 1970; Arreguín-Sánchez, 1987), however, remains essentially unregulated. Important in formulating management plans for marine fish species such as red grouper is information on population structure or stocks and on levels of genetic variation. This information is critical for both stock assessment and adjustment of fishery regulations within regions.

In a previous study (Richardson and Gold, 1993), we examined mitochondrial (mt)DNA variation among a sample of red grouper from the west coast of Florida. Estimated within-population mtDNA diversity in this sample was among the lowest reported for a marine fish species. In this note, we report mtDNA variation within a sample of red grouper from the Campeche Banks, Mexico (Fig. 1). The main objectives were 1) to determine whether red grouper from Florida and Mexico represent different genetic stocks and 2) to compare levels of mtDNA diversity in red grouper from Campeche Banks, Mexico, with those from west Florida.

Materials and methods

Specimens were obtained from commercial fishermen in Celestún and San Felípe, Mexico, during November, 1991 (Fig. 1). Heart and muscle tissue were removed from each individual, stored at –20°C in a fish house in Merida, Mexico, and transported on wet ice to Houston, Texas, where they were frozen in liquid nitrogen. Upon arrival at Texas A&M, tissues were stored at –80°C.

Details of DNA isolation, storage, restriction enzyme digestion, agarose electrophoresis of DNA fragments, and Southern blot hybridization with a mtDNA probe may be found in Gold and Richardson (1991). The mtDNA probe used (λEm-mt2) was an entire red grouper mtDNA genome cloned into lambda bacteriophage (Richardson and Gold, 1993). The ten restriction endonucleases used in this study were those previously identified to be polymorphic in red grouper (Richardson and Gold, 1993) and included *Apa*I, *Kpn*I, *Nco*I, *Nde*I, *Nhe*I, *Nsi*I, *Pvu*II, *Ssp*I, *Xba*I, and *Xmn*I.

Within-sample mtDNA diversity was assessed by nucleon diversity (probability that any two individuals drawn at random will differ in mtDNA haplotype) and by intrapopulational nucleotide sequence diversity (average nucleotide difference between any two individuals drawn at random). Both estimates of mtDNA diversity were generated by using equations in Nei and Tajima (1981).

Geographic partitioning of mtDNA variation was assessed by homogeneity testing of mtDNA haplotype frequencies and by searching for phylogeographic cohesion or structure of mtDNA haplotypes with a parsimony approach. Homogeneity tests included 1) a log-likelihood (G) test and 2) a Monte Carlo randomization procedure developed by Roff and Bentzen (1989). Analyses were carried out with the BIOM-PC (a package of statistical programs, Applied Biostatistics Inc.; Rohlf, 1987) and REAP (restriction en-

* This paper represents number XV in the series "Genetic studies in marine fishes" and contribution number 48 of the Center for Biosystematics and Biodiversity at Texas A&M University, College Station, Texas 77843-2258.

Manuscript accepted 25 July 1996.
Fishery Bulletin 95:174–179 (1997).

Figure 1
Sampling localities of red grouper (*Epinephelus morio*).

zyme analysis package; McElroy et al., 1992) computer software packages. A minimum-length parsimony network of mtDNA haplotypes was constructed by connecting haplotypes in increments of (inferred) single site gains and losses.

Results

Digestion patterns of the ten restriction enzymes revealed 16 mtDNA haplotypes among all red grouper assayed to date (exclusive of the five individuals from the Dry Tortugas sampled by Richardson and Gold [1993, Table 1]). Of the 16 mtDNA haplotypes, one (haplotype 1) accounted for 77% of all individuals sampled. Four haplotypes were present in both geographic regions. The remaining 12 haplotypes were unique to a geographic region (Table 1). Percentage nucleotide sequence divergence between individual haplotypes ranged from 0.09 to 0.59 (mean $\pm$SE = 0.27 $\pm$0.01).

MtDNA nucleon diversity among individuals from the Campeche Banks was 0.365. This value is lower than that found among individuals from the west coast of Florida (0.457). Percentage intrapopulational nucleotide sequence diversity among individuals from the Campeche Banks was 0.042 $\pm$ 0.001 (mean $\pm$ SE), as compared with 0.078 $\pm$ 0.003 among individuals from the west coast of Florida. Nucleon and intrapopulational nucleotide sequence diversities among all red grouper assayed to date are 0.389 and 0.059 $\pm$ 0.001, respectively. Values obtained are based on the 28 restriction enzymes surveyed by Richardson and Gold (1993) and on the assumption that the restriction enzymes previously found to be monomorphic among red grouper from the west coast of Florida are monomorphic among red grouper from Mexico as well.

Results of tests for homogeneity of mtDNA haplotype frequencies between the two localities were nonsignificant (G=20.02, P≈0.21 and χ^2=14.71, P=0.55). The parsimony network (Fig. 2) included a single "assumed" haplotype (i.e. one not detected in the survey). All the haplotypes in the network, including the "assumed" haplotype, could be derived from adjacent haplotypes by one or two restriction site changes. The most common haplotype (haplotype 1) was considered to be central, and nine of the remaining 14 haplotypes were derived from the central haplotype by a single restriction site change. Haplotypes 5 and 8 are most divergent and are separated from the common haplotype by 4 restriction site changes. Except for haplotypes 5 and 8, and 6 and 7 (all from Campeche Banks, Mexico) which are grouped by a single restriction site change, no geographic partitioning was evident.

Table 1
Distribution of 16 mitochondrial DNA composite genotypes (haplotypes).

Haplotype number	Composite MtDNA genotype[1]	Locality	
		Campeche Banks	West Florida Shelf
1	AAAAAAAAAA	43	34
2	AAABAAAAAA	1	1
3	AAAAAAAAAB	3	2
4	AAAABAAAAA	1	1
5	ABAAAABAAC	—	1
6	AAAAAABAAA	—	1
7	AABAAABAAA	—	1
8	ABAAAABCAB	—	1
9	CAAAAAAAAA	—	1
10	AAAAABAAAA	—	1
11	AAAAAAABBA	—	1
12	BAAAAAAAAB	—	1
13	AAAACAAAAA	2	—
14	ACAAAAAAAA	2	—
15	AAAAAAADAB	1	—
16	AAAAAAABAA	1	—

[1] Letters (from left to right) are digestion patterns for *Apa*I, *Kpn*I, *Nco*I, *Nde*I, *Nhe*I, *Nsi*I, *Pvu*II, *Ssp*I, *Xba*I, and *Xmn*I. Restriction fragment sizes may be found in Richardson and Gold (1993). Fragment sizes for three restriction fragment patterns not previously identified are as follows: (in base pairs) *Kpn*I(C): 16800; *Nhe*I(C): 6800, 3200, 2950, 2450, 1300, 50; and *Ssp*I(D): 6000, 5400, 2900, 1700, 800.

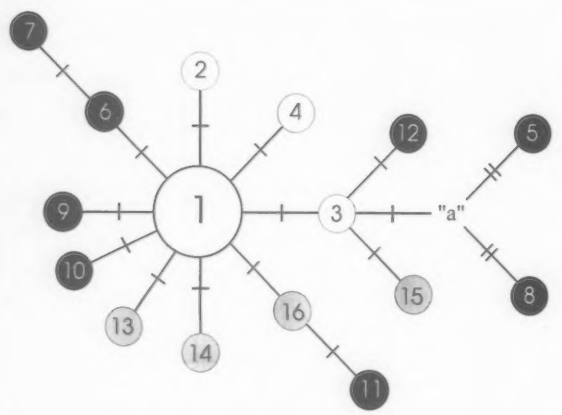


Figure 2

Minimum-length parsimony network of red grouper mitochondrial DNA haplotypes. Numbers refer to mtDNA haplotypes listed in Table 1. Hatch marks represent the number of restriction site changes among individual haplotypes. The haplotype designated by "a" refers to a haplotype assumed to exist, but not detected in the survey. Shaded and solid circles refer to haplotypes unique to a locality (West Florida Shelf and Campeche Banks respectively). Open circles are haplotypes found in both localities.

Discussion

Homogeneity in mtDNA haplotype frequency and absence of phylogeograhic structure among haplotypes are consistent with the hypothesis that red grouper from the west Florida shelf and the Campeche Banks represent a single unit stock. There are caveats to this hypothesis. First, genetic homogeneity does not unequivocally establish occurrence of a unit stock, in part because proof of a null hypothesis is impossible. Genetic homogeneity in this case is simply consistent with the hypothesis that samples are drawn from a single population with the same parametric haplotype frequencies. In addition, small amounts of gene flow are sufficient to homogenize populations genetically (Allendorf and Phelps, 1981), even though geographic samples may be discontinuous demographically. Another caveat is that observed homogeneity may reflect historical rather than current events. Present-day populations could be isolated spatially but have had enough contact in the recent past such that haplotype frequencies are overshadowed by historical gene flow. Examination of a more rapidly evolving nuclear marker (e.g. microsatellite loci) may provide data that suggest such a scenario.

Within-population mtDNA diversity among red grouper from the Campeche Banks was lower than that reported previously for red grouper from the west Florida shelf, and overall, red grouper have among the lowest levels of mtDNA diversity reported for marine fish species (Table 2). Levels of intrapopulational mtDNA diversity are thought to reflect evolutionary-effective population sizes of females (Avise et al., 1988), although there is some evidence (Gold et al., 1994) that intrapopulational mtDNA diversities may also reflect contemporary (female) population sizes as well. The latter is of interest given that some of the species with low intrapopulational mtDNA diversities (e.g. weakfish, orange roughy) have experienced significant reductions in population sizes over the past several years (Graves et al., 1992b; Smolenski et al., 1993). The mtDNA diversity observed in red grouper may thus indicate that red grouper warrant immediate attention in terms of management regulation. Alternatively, red grouper and black sea basses, the species with the lowest reported mtDNA diversities (Table 2), are protogynous hermaphrodites (Manooch, 1988), and it is possible that this mode of reproduction may affect estimates of mtDNA diversity. Estimates for black sea bass (Bowen and Avise, 1990), however, may be somewhat compromised by the low sample sizes, given that a significant proportion of the sampling variance for estimates of nucleotide diversity stems from population sampling (Lynch and Crease, 1990). Further study of mtDNA diversity in other hermaphroditic fishes and in sea bass is clearly warranted.

Present-day gene flow

The observed genetic homogeneity in *E. morio* from west Florida and Mexico was surprising because, a priori, we expected gene flow between the two areas to be minimal and the two populations to be divergent in mtDNA haplotypes. This expectation was based on available information about the life history of red grouper and on reported discontinuity in red grouper distribution. Observations from divers and aquaria personnel have shown that juvenile red grouper are fairly sedentary, preferring to hide in crevices or shells of shallow nearshore habitat (Moe, 1969). Adult red grouper also are important members of the benthic community, frequently occupying crevices, ledges, and caverns formed by rugged limestone reefs. There is, however, evidence that red grouper do migrate at least to some extent, and tagging data suggest "developmental" migration from shallow coastal waters to depths greater than 36 m at approximately 5 years of age (Moe, 1966, 1967;

Table 2

Comparison of estimates of intrapopulational mtDNA diversity in various species of marine fishes.

Species	Number of individuals surveyed	Number of mtDNA haplotypes	Nucleotide sequence diversity (%)
Bluefish[1]	372	40	1.23
Atlantic herring[2]	69	26	1.09
Gulf Menhaden[3]	16	16	0.99
Red drum[4]	693	99	0.88
Spanish sardine[5]	73	24	0.52
Red snapper[4]	421	68	0.50
Black drum[4]	300	37	0.48
Greater amberjack[6]	59	23	0.34
Spotted seatrout[7]	384	73	0.31
Orange roughy[8]	244	22	0.13
Weakfish[9]	370	11	0.13
Red grouper	105[10]	16	0.05[11]
Atlantic black sea bass[2]	19	3	0.03
Gulf black sea bass[2]	9	2	0.03

[1] Graves et al., 1992a.
[2] Kornfield and Bogdanowicz, 1987.
[3] Bowen and Avise, 1990.
[4] Gold et al., 1994.
[5] Tringali and Wilson, 1993.
[6] Richardson and Gold, 1993.
[7] Gold, J. R. 1995. Dep. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, TX 77843-2258. Unpubl. data.
[8] Smolenski et al., 1993.
[9] Graves et al., 1992b.
[10] Number of individuals includes 5 additional specimens from the Dry Tortugas surveyed by Richardson and Gold (1993).
[11] Value obtained by using 28 restriction enzymes surveyed in Richardson and Gold (1993). Value obtained from the ten polymorphic restriction enzymes surveyed here is 0.15.

Beaumariage[1]). Presumably, this migration corresponds to the onset of sexual maturity. Other tagging data (Moe, 1966) suggest that adult red grouper may move as much as 18 to 50 miles over a period of time from several months to a year. Finally, on the basis of data from other species of *Epinephelus* (Mito et al., 1967), the pelagic larval stage in *E. morio* is presumed to last 30–40 days, during which larvae are dispersed by ocean currents along a great portion of the Florida shelf (Moe, 1969). However, despite the evidence suggesting that individual red grouper could move considerable distances, consistent patterns of migration in red grouper are not reported, and it is generally presumed that adult red grouper do not undergo large-scale movements offshore.

Gene flow between the west Florida shelf and the Campeche Banks via migration of adults would have to occur either 1) along the north-central and western Gulf or 2) across the Florida Straights. Rivas (1970) noted circumstantial evidence suggesting that there may be seasonal migration of red grouper between the northern and southern Gulf, most probably via a western route. Red grouper, however, are rarely taken in the Gulf west of the Mobile Basin (Springer and Bullis, 1956), and virtually no landings of red grouper occur along most of the Texas coast (Osburn[2]; Campbell[3]). The apparent paucity of red grouper in the northwestern Gulf may reflect either the absence of suitable habitat along the Texas–Louisiana shelf or be a result of some other extrinsic barrier (McEachran[4]). These observations suggest that movement of adult red grouper through the western Gulf is unlikely, if it occurs at all. With respect to movement across the Florida Straights, Rivas (1970) considered it unlikely that red grouper, a bottom dwelling fish, would cross great depths. The Florida Straights are characterized by 100 to 2,000 fathom depths that separate the Campeche Banks from the west Florida shelf (Rezak et al., 1985). This range also suggests limited movement, if any, of red grouper from west Florida to the Campeche Banks.

Alternatively, present-day gene flow among red grouper could occur through dispersal of larvae by ocean currents. Shulman and Bermingham (1995) recently examined variation in mtDNA data among eight species of reef-associated fishes and searched for correlations between gene flow and egg type (pelagic and nonpelagic) and length of planktonic (usually larval) life, two life history traits which could potentialy affect dispersal capability. Although surface currents that might explain observed genetic homogeneity in five of the species were identified, neither egg type nor length of larval stage appeared to be an adequate predictor of geographic structure in reef associated fishes (Shulman and Bermingham, 1995). Therefore, even though red grouper may have

[1] Beaumariage, D. S. 1969. Returns from the 1965 Schlitz tagging program including a cumulative analysis of previous results. Fla. Dept. Nat. Resources, Mar. Res. Lab., Tech. Ser. No. 59:1–38. Div. of Mar. Resources, Dep. of Environmental Protection, Florida Mar. Res. Inst., 100 Eighth Ave. SE, St. Petersburg, FL 33701.

[2] Osburn, H. R. 1988. Trends in finfish landings by sport-boat fishermen in Texas marine waters, May 1974–May 1987. Texas Parks Wildl. Dep., Manag. Data Ser., no. 150, Austin, TX. Fisheries and Wildlife Div., Coastal Fisheries Branch, Texas Parks and Wildlife Dep., 4200 Smith School Road, Austin, TX 78744.

[3] Campbell, R. P. 1993. Trends in Texas commercial fishery landings, 1972–1992. Texas Parks Wildl. Dep., Manag. Data Ser., no. 106, Austin, TX. Fisheries and Wildlife Div., Coastal Fisheries Branch, Texas Parks and Wildlife Dep., 4200 Smith School Road, Austin, TX 78744.

[4] McEachran, J. D. 1995. Dep. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, TX 77843-2258. Personal commun.

a lengthy pelagic larval stage, there is no reason to assume a priori that gene flow occurs via dispersal of red grouper larvae. Nonetheless, it cannot be ruled out as a contributing factor.

Historical bottleneck

In a general sense, genetic homogeneity and absence of phylogenetic structure are compatible with limited gene flow under models where isolated populations (or subpopulations) have recently diverged from a panmictic population that possessed low levels of genetic variation and where each subpopulation has a small effective population size. An example of isolated subpopulations that are genetically homogeneous and also genetically depauperate are African cheetahs, where subspecies in east and south Africa are essentially monomorphic for the same alleles at numerous genetic loci (O'Brien et al., 1987). To account for both genetic homogeneity between, and low genetic variability within, subpopulations, O'Brien et al. (1987) hypothesized the past occurrence of at least two genetic bottlenecks. Their hypothesis was based on the premise that genetic homogeneity of isolated subpopulations was consistent with a historical event; whereas low genetic variability in extant populations was consistent with a more recent event.

Red grouper fit the cheetah model in that the subpopulations surveyed are genetically homogeneous and each possesses limited genetic variation. We suggest the possibility that red grouper from west Florida and Mexico are isolated genetically, but that recurring genetic bottlenecks continue to generate high frequencies of the most common genotype. In addition, we suggest that red grouper from these two regions were not isolated historically and that the historical population underwent a severe bottleneck that reduced much of the extant genetic variation. These suggestions account for the observed genetic data and how isolated populations can be genetically homogeneous. A historical bottleneck could have occurred during late Pleistocene times when environmental fluctuations impacted the biota of the region (Rezak et al., 1985; Graham and Mead, 1987). Our suggestions could be tested, in part, by asking whether rare haplotypes found in both locals are identical by descent (i.e. independently derived). In red grouper, two of the three haplotypes shared between west Florida and Campeche Banks are the result of a site loss from the common haplotype and could be the result of a nucleotide substitution at any one of six nucleotide positions. Examination of a more rapidly evolving nuclear marker in individuals from each locality that share these rare haplotypes would address this issue.

Acknowledgments

We thank C. Furman and K. Burns for help in procuring specimens of red grouper from Mexico. Work was supported by the Marfin Program of the U.S. Department of Commerce Award NA90AA-H-MF755, administered by the National Marine Fisheries Service and by the Texas Agricultural Experiment Station under Project H-6703. Part of the work was carried out in the Center for Biosystematics and Biodiversity, a facility funded, in part, by the National Science Foundation under grant DIR-8907006.

Literature cited

Allendorf, F. W., and S. R. Phelps.
1981. Use of allelic frequencies to describe population structure. Can. J. Fish. Aquat. Sci. 38:1507–1514.

Arreguín-Sánchez, F.
1987. Present status of red grouper fishery of the Campeche Bank. Proc. Gulf Caribb. Fish. Inst. 37:498–509.

Avise, J. C., R. M. Ball, and J. Arnold.
1988. Current versus historical population sizes in vertebrate species with high gene flow: a comparison based on mitochondrial DNA lineages and inbreeding theory for neutral mutations. Mol. Biol. Evol. 5: 331–344.

Bowen, B. W., and J. C. Avise.
1990. Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: influence of zoogeographic factors and life-history patterns. Mar. Biol. 107:371–381.

Brulé, T., and L. G. Rodriguez Canché.
1993. Food habits of juvenile red groupers, *Epinephelus morio* (Valenciennes, 1828), from Campeche Bank, Yucatan, Mexico. Bull. Mar. Sci. 52:772–779.

Gold, J. R., and L. R. Richardson.
1991. Genetic studies in marine fishes. IV. An analysis of population structure in the red drum (*Sciaenops ocellatus*) using mitochondrial DNA Fish. Res. 12:213–241.

Gold , J. R., L. R. Richardson, C. Furman, and F. Sun.
1994. Mitochondrial DNA diversity and population structure in marine fish species from the Gulf of Mexico. Can. J. Fish. Aquat. Sci. 51:205–214.

Graham, R. W., and J. I. Mead.
1987. Environmental fluctuations and evolution of mammalian faunas during the last deglaciation in North America. *In* W. F. Ruddiman and H. E. Wright (eds.), North America and adjacent oceans during the last deglaciation, p. 371–402. Geological Society of America, Boulder, CO.

Graves, J. E., J. R. McDowel, A. M. Beardsley, and D. R. Scoles.
1992a. Stock structure of the bluefish *Pomatomus saltatrix* along the mid-Atlantic coast. Fish. Bull. 90:703–710.

Graves, J. E., J. R. McDowell, and M. L Jones.
1992b. A genetic analysis of weakfish, *Cynoscion regalis*, stock structure along the Mid-Atlantic coast. Fish. Bull. 90:469–475.

Kornfield, I., and S. M. Bogdanowicz.
1987. Differentiation of mitochondrial DNA in Atlantic herring, *Clupea harengus*. Fish. Bull. 85:561–568.

Lynch, M., and T. J. Crease.
1990. The analysis of population survey data on sequence variation. Mol. Biol. Evol. 7:377–394.

Manooch, C. S., III.
1988. Fisherman's guide to the fishes of the southeastern United States. NC State Mus. Nat. Hist., Raleigh, NC.

McElroy, D., P. Moran, E. Bermingham, and I. Kornfield.
1992. REAP-The Restriction Enzyme Analysis Package. J. Hered. 83:157–158.

Mito, S., M. Ukawa, and M. Higuchi.
1967. On the larval and young ages of a serranid fish, *Epinephelus akaara* (Temminck et Schegel). Bull. Naikai Region. Fish. Res. Lab. 25:337–347.

Moe, M. A.
1966. Tagging fish in Florida offshore waters. Fla. Bd. Conserv., Prof. Papers Ser., no. 4, 117 p.
1967. Prolonged survival and migration of three tagged reef fishes in the Gulf of Mexcio. Trans. Am. Fish. Soc. 96: 228–229.
1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Prof. Pap. Ser. Fla. Dep. Nat. Resour. Mar. Sci. Lab. 34:1–331.

Nei, M., and F. Tajima.
1981. DNA polymorphism detectable by restriction endonucleases. Genetics 97:145–163.

O'Brien, S. J., D. E. Wildt, B. Mitchell, T. M. Caro, C. FitzGibbon, I. Aggundey, and R. E. Leakey.
1987. East African cheetahs: Evidence for two population bottlenecks? Proc. Natl. Acad. Sci. 84:508–511.

Rezak, R., T. J. Bright, and D. W. McGrail.
1985. Reefs and banks of the northwestern Gulf of Mexico. John Wiley and Sons Inc., NY, 259 p.

Richardson, L. R., and J. R. Gold.
1993. Mitochondrial DNA variation in red grouper (*Epinephelus morio*) and greater amberjack (*Seriola dumerili*) from the Gulf of Mexico. ICES J. Mar. Sci. 50:53–62.

Rivas, L. R.
1970. The red grouper of the Gulf of Mexico. Commer. Fish. Rev. 32:24–30.

Roff, D. A., and P. Bentzen.
1989. The statistical analysis of mitochondrial polymorphisms: chi-square and the problem of small samples. Mol. Biol. Evol. 6:539–545.

Rohlf, F. J.
1987. BIOM: A package of statistical programs to accompany the text Biometry. Applied Biostatistics, Inc. Setauket, NY, 70 p.

Shulman, M. J., and E. Bermingham.
1995. Early life histories, ocean currents, and the population genetics of caribbean reef fishes. Evol. 49:897–910.

Smith, C. L.
1961. Synopsis of biological data on grouper (*Epinephelus* and allied genera) of the western North Atlantic. FAO Fish. Bio. Synop. 23:1–61.

Smolenski, A. J., J. R. Ovenden, and R. W. G. White.
1993. Evidence of stock separation in southern hemisphere orange roughy (*Hoplostethus atlanticus*, Trachichthyidae) from restriction-enzyme analysis of mitochondrial DNA. Mar. Biol. 116:219–230.

Solís Ramírez, M.
1970. The red grouper fishery of Yucatan Peninsula, Mexico. Proc. Gulf Caribb. Fish. Inst. 22:122–129.

Springer, S., and H. R. Bullis.
1956. Collections by the *Oregon* in the Gulf of Mexico. Sci. Rep. U.S. Fish. Wildl. Serv., no. 196:1–134.

Tringali, M. D., and R. R. Wilson Jr.
1993. Differences in haplotype frequencies of mtDNA of the spanish sardine, *Sardinella aurita*, between specimens from the eastern Gulf of Mexico and southern Brazil. Fish. Bull. 91:362–370.

Entanglement of California sea lions, *Zalophus californianus californianus*, in fishing gear in the central-northern part of the Gulf of California, Mexico

Alfredo Zavala-González
Eric Mellink
Departamento de Ecología, Centro de Investigación Científica y de Educación Superior de Ensenada
Apdo. Postal 2732, Ensenada, Baja California, México
U.S. mailing address: CICESE; P.O. Box 434844, San Diego, CA 92143
E-mail address: alzago@cicese.mx

The range of the California sea lion, *Zalophus californianus californianus*, extends from British Columbia south to Mazatlan, Mexico, and includes the Gulf of California. The population of sea lions in Mexico has been estimated at 74,467 individuals along the Pacific coast (Lowry et al.[1]), 28,220 in the Gulf of California (Zavala, 1990). Little is known about the Pacific coast population, but there are probably 8 breeding colonies (Lowry et al., 1992). In the Gulf there are 40 rookeries: 13 breeding colonies and 27 haulouts (Zavala et al., in press). Strong tidal forces cause a constant upwelling condition in the central-northern part of the Gulf of California that sustains high nutrient and phytoplankton concentrations, especially around the Midriff Islands in the central Gulf (Alvarez-Borrego, 1983; Alvarez-Borrego and Lara-Lara, 1991). This upwelling condition allows the existence of large populations of fish, marine mammals, and marine birds.

Between the 1960's and the 1980's, the population at some breeding colonies of California sea lions in the Gulf of California increased 30% (Le Boeuf et al., 1983). During the 1980's and early 1990's, the yearly increase in those populations was between 2% (Morales, 1990; Zavala et al., in press) and 4.7% (Aurioles and Arizpe[2]). After 1991 some populations experienced a slight reduction in size and later a partial recovery (Heath et al., 1994; Zavala et al.[3]).

Since 1985, we have censused annually 10 of the 11 reproductive sea lion colonies that account for 94.9% of all sea lions in the Gulf of California (Fig. 1 in Aurioles and Zavala, 1994). In 1991 we commenced seeing more sea lions with pieces of fishing gear entangled around their head and neck than we had remembered seeing during previous years (Zavala and García[4]) and began documenting the incidence of entanglement. We report the numbers of entangled sea lions observed between 1991 and 1995 in the central-northern part of the Gulf of California and comment on the effect this may have on the conservation of the species.

Methods

Ten of 11 breeding colonies in the central-northern Gulf of California were studied (Fig. 1). Only Roca Consag (31°12'N, 114°29'W) was excluded. Between 1991 and 1995, we made eight cruises to the 10 breeding colonies: 16 Jun–19 Jul 1991, 8 Jul–4 Aug 1992, 16–25 Jun 1993, 10–29 Jul 1993, 16–25 Jun 1994, 11–20 Jul 1994, 1–4 Aug 1994, and 15–28 Jun 1995. San Jorge and El Coloradito were visited only once each year whereas Los Cantiles and San Pedro Mártir were not surveyed in 1991 and 1992, respectively. All other islands were surveyed on every trip.

All cruises were made on patrol ships of the Mexican Navy, leaving from Guaymas, Sonora. Surveys around the islands were made aboard small (7 m in length) fiberglass boats with 35–55 hp outboard motors. We cruised at about 2 knots, 30–50 m from the coast, to census the animals. They were classified as adult males, subadult males, females, juveniles, or pups (sensu LeBoeuf et al., 1983; Aurioles and Zavala, 1994).

Entanglement frequencies were calculated by dividing the total number of entangled animals (those animals with pieces of fishing gear around head and neck) by the total number of adult, subadult, and

[1] Lowry, M. S., P. Boveng, R. J. DeLong, Ch. W. Oliver, B. S. Stewart, H. DeAnda, and J. Barlow. 1992. Status of California sea lion (*Zalophus californianus californianus*) population in 1992. Admin. Rep. LJ-92-32, 35 p. Southwest Fisheries Science Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2] Aurioles, D., and O. Arizpe. 1989. Unpubl. data. Departamento de Pesquerías y Biología Marina. Centro Interdisciplinario de Ciencias Marinas. Apdo. Postal 592, La Paz, B.C.S., México.

[3] Zavala, A., H. de la Cueva, and E. Mellink. 1991. Unpubl. data. Departamento de Ecología, Centro de Investigación Científica y Educación Superior de Ensenada, Apdo. Postal 2732, Ensenada, B.C., México.

[4] Zavala, A., and M. C. Garcia. 1991. Departamento de Ecologia, Centro de Investigación Cientifica y Educación Superior de Ensenada, Apdo. Postal 2732, Ensenada, Baha California, México. Personal obs.

Manuscript accepted 4 September 1996.
Fishery Bulletin 95:180–184 (1997).

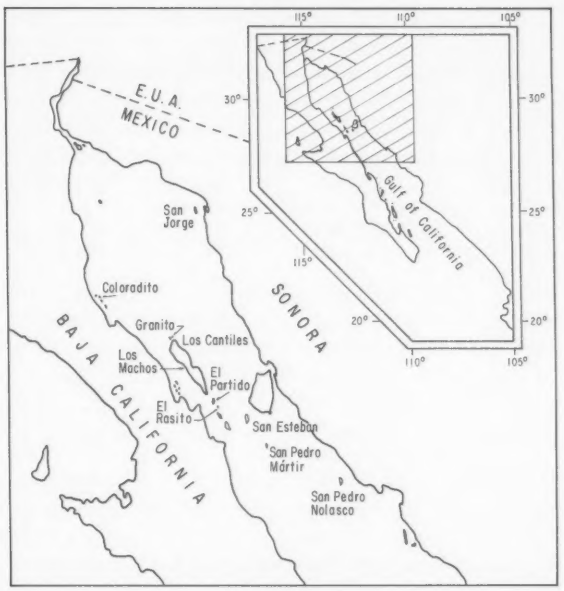


Figure 1
Central-northern Gulf of California, showing the study localities.

young animals. We excluded dead animals because time since death could not be assessed. Pups spend most of their time on land and have virtually no interaction with fishing gear during the survey periods. When we made more than one survey per year, we considered the highest rate of entanglement as the best estimator.

We used the "differences-between-proportions" test (Zar, 1974) to compare the proportions of age and sex classes between the entangled animals and the population. Differences between sea lion colonies and years were compared by using a two-factor Analysis of Variance (ANOVA) and Newman-Keuls (N-K) tests (Zar, 1974) on the basis of the number of entangled animals (adjusted by a square-root transformation) and entanglement rates (adjusted by an arcsine transformation). Variation in the number of entangled animals and in the average transformed entanglement rates over time, as well as the relationship between number of entangled animals and colony size, were analyzed with simple linear regressions (Zar, 1974).

In the two cases where we lacked data, we used the eight colonies, for which we had complete information, to calculate the relationship between the year with missing data (1991 or 1992) and the average of the remaining four years,and then used the average of the problem colony (Los Cantiles or San Pedro Mártir) to estimate the missing value. This was done in order to perform the statistical tests on a standard basis.

Types of fishing gear involved were recorded from dead entangled animals. This information was completed with records about the size and characteristics of the fishing gear used by fishermen working in the islands. Similarly, fishing gear debris found on sea lion rookeries and showing evident signs of having been associated with a sea lion (bites, sea lion fat,) was noted. We also interviewed local fishermen about their problems with sea lions.

Results and discussion

Sea lion entanglement

During the study, we counted 237 entangled animals (Table 1), 207 of which could be assigned to a particular sex and age class: 46.4% were young animals (1–3 yr), 41.5% females, 7.2% subadult males, and 4.8% adult males. The percentage of young animals among the entangled animals was statistically higher than their proportion in the censused population (25.8%, Z=6.70, P=7.13×10^{-11}), whereas that of females was lower (60.5%, Z=–5.53, P=0.913×10^{-8}). This is probably a result of young animals being more curious, less experienced, and weaker, in addition to foraging closer to the surface (senior author, personal observation [1994–95]). In other species (northern fur seals, *Callorhinus ursinus*) high rates of juvenile mortality might have caused a decrease in the population (Trites, 1992). Our data are not sufficient to establish or discard any such links. Percentages of entanglement of subadult and adult males were not different from percentages of proportion of subadult and adult males in the population (6.3%, Z=0.78, P=0.294 and 7.4%, Z=1.5, P=0.13, respectively).

Between 1991 and 1995, the number of recorded entangled sea lions for all 10 rookeries combined varied from 34 (±2.27, 95% CI) (adjusted to 36) to 72, with a low of 24 (±4.02, 95% CI) (adjusted to 27) in 1992 (Table 1). Regression analysis between number of entangled animals and year was significant (n=5, r^2=0.79, F=11.05, P=0.045). Significant differences were found only between 1992 and 1995: the other years were not different from one other (F=3.09, P=0.027).

In 1992, there were not only fewer entangled animals, but also there were fewer sites with entangled animals. This year saw the worst recent fishing season in the central Gulf according to information at the Bahía de Los Ángeles fishing office, and this finding is likely a reflection of the prevailing El Niño Southern Oscillation conditions, which had strong

Table 1

Number of entangled and total (in parentheses, including entangled) California sea lions, except pups, in 10 breeding colonies in the central-northern Gulf of California, 1991–95.

	Locations		Year				
Rookeries	Lat.	Long.	1991	1992	1993	1994	1995
San Jorge	31°01'N	113°15'W	8 (4,536)	14 (2,915)	10 (2,183)	4 (2,208)	24 (3,200)
Coloradito	30°03'N	114°29'W	4 (2,100)	2 (1,610)	7 (1,662)	3 (1,749)	13 (1,688)
Granito	29°34'N	113°33'W	2 (609)	1 (603)	6 (390)	2 (923)	4 (631)
Los Cantiles	29°32'N	113°29'W	—	1 (712)	3 (620)	1 (602)	6 (916)
Los Machos	29°18'N	113°31'W	0 (718)	0 (601)	1 (718)	4 (659)	1 (512)
El Partido	28°53'N	113°02'W	5 (463)	2 (524)	4 (798)	3 (311)	1 (402)
El Rasito	28°49'N	113°00'W	1 (353)	0 (326)	1 (101)	5 (223)	0 (198)
San Esteban	28°43'N	112°35'W	10 (4,758)	4 (3,135)	10 (2,610)	20 (3,859)	14 (3,396)
S.P. Mártir	28°23'N	112°20'W	1 (1,379)	—	11 (676)	8 (770)	7 (937)
S.P. Nolasco	27°58'N	111°23'W	3 (1,009)	0 (338)	1 (517)	3 (340)	2 (358)
Total			34 (15,925)	24 (10,764)	54 (10,275)	53 (11,644)	72 (12,238)

effects in the Gulf (Hamman et al., 1995). Entanglement rate did not exhibit any tendency through time (n=5, r^2=0.44, F=2.35, P=0.223), and the ANOVA detected only 1992 as statistically inferior to 1993 and 1994, whereas 1991 and 1995 were not different from any other year (F=4.20, P=0.007).

San Jorge and San Esteban exhibited the largest overall numbers of sea lions (>2,000 California sea lions) (Table 1); El Coloradito had intermediate values (>1500, <2200), and the other colonies ≤1400 sea lions.The ANOVA indicated that the first two sites had statistically more entangled sea lions than did El Partido, Granito, Cantiles, San Pedro Nolasco, El Rasito, and Los Machos, whereas San Pedro Mártir and El Coloradito were not different from any other site (F=7.67, P<0.001). This pattern corresponds to differences in the size of the colonies; a regression linking total number of entangled animals at each colony and size of the different colonies was highly significant (n=10, r^2=0.92, F=89.71, P<0.001).

We have no detailed records of differences in the fishing effort throughout the study area, although it seems to be larger in the Midriff region than in the northern Gulf (E. Mellink, personal obs. [1995]). The ANOVA did not show differences in the entanglement rates between colonies (F=0.64, P=0.76), and the number of incidents seemed to be more a function of the size of the colony than of local and yearly variations in fishing effort, although, as suggested by the 1992 data, these effects cannot be neglected.

Entanglement rates in our region varied between 0% and 2.24%. These values are substantially lower than the 3.9–7.9% detected in Los Islotes, Bahía de La Paz, in the southern Gulf of California (24°35'N, 110°23'W; Harcourt et al., 1994). In the latter locality, high values may have been due to the proximity of Los Islotes to a moderate-size city (La Paz, approx. 250,000 inhabitants) and to abundant sport and commercial fishing. However, our entanglement values are higher than those at California islands (0.08%, Stewart and Yochem, 1987) and, again, this could be due to differences in the intensity and type of fishing practiced.

The main fishing gear involved in sea lion entanglement in the study area were nets and, to a lesser degree, lines and ropes. The nets included monofilament, purse seine, and gill nets (with stretched mesh sizes 3", 3.2", 4,5", 5", and 8"), cotton gill nets (1.5" and 5.1" mesh size), and trammel nets (either cotton or nylon monofilament with 14" to 16" mesh size). These nets originally measure 120–180 fathoms long and 7 fathoms high. The lines involved were all nylon of different thickness and, in most cases, were found tied around the animal. In only one case did we see a hook in a sea lion's mouth, or a line coming out of it.

Most entanglement occurs during fishing, either when the net and the catch are hauled out or when a net is deployed during 24–48 hr periods. In other regions of the North Pacific, in addition to entanglement during events involving active fishing, entanglement occurs because marine mammals encounter drifting debris, especially when they are foraging or migrating (Fowler, 1987). In the central-northern Gulf of California it is rare to encounter fishing gear debris drifting in the water. Artesanal fishermen, who carry out most of the fishing in the area, cannot afford to lose nets; therefore nets are usually fixed, not drifted. When part of a net or a complete net is no longer usable, it is usually discarded in a local gar-

bage dump. When a fisherman finds a lost drifting net at sea, he takes it for his own use. Unlike other areas of the world (Croxall et al., 1990) and the southern Gulf of California (Harcourt et al., 1994), the central-northern portion of the Gulf of California did not provide evidence of sea lions entangled in nonfishing plastic debris.

Sea lion conservation

In addition to accidental entanglements reported here, there is a deliberate (although illegal) killing of sea lions in the region for baiting shark longlines. At Isla San Pedro Mártir, Thomson and Mesnick[5] found 14 sea lions entangled in a gill net in a cave about 15–20 m from a breeding site, in July 1993. They concluded that the net had been set to intentionally capture sea lions. In December 1993, about 20 sea lions were captured in a gill net in San Pedro Nolasco (El Imparcial, Hermosillo, Sonora, 25 December 1993). The fishermen involved argued that the capture had been accidental, resulting from their lack of expertise. In addition to their intentional capture, sea lions are sometimes shot with firearms because fishermen believe that they interfere with fishing gear (Delgado-Estrella et al., 1994).

Our data were limited to a single season in each year of a 5-yr span and did not include animals that died without us having seen them on the islands. However, according to our assessment, the current entanglements rate of 0.49% does not seem to pose a threat to the conservation of California sea lions in the central-northern Gulf of California. We believe, however, that entanglement should be routinely monitored and studied in further detail.

Acknowledgments

María del Carmen García, Elisa Peresbarbosa, Leonardo Inclán, María Concepción García, Jaime Luévano, Martín Escoto, Luis Bourillón, María de la Soledad Tordecillas, Sarah Mesnick, Carlos Godínez, Dulce María Broussett, and several students from the Laboratorio de Mamíferos Marinos, Facultad de Ciencias, Universidad Nacional Autónoma de México, assisted with field work. Oscar Sosa, Gregory Hamman, Fred Julian, Mark Lowry, and Tim Gerrodette provided editorial assistance. All cruises and surveys were carried out with the support of the Armada de México (6ta Zona Naval), to which we are greatly in debt. Consejo Nacional de Ciencia y Tecnología (México) supported A. Zavala with an academic scholarship and partially supported this project through a grant to E. Mellink. The Oficina Federal de Pesca in Baja California kindly provided fishing records for Bahía de los Angeles. All work was carried out under permits from the Dirección General de Aprovechamiento Ecológico de los Recursos Naturales, Instituto Nacional de Ecología.

[5] Thomson, D. A., and S. L. Mesnick. 1993. Biodiversity of the marine fauna around islands in the Gulf of California. Unpubl. report, Department of Ecology and Evolutionary Biology, Univ. Arizona, Tucson, AR.

Literature cited

Alvarez-Borrego, S.
1983. The Gulf of California. *In* B. H. Ketchum (ed.), Estuaries and enclosed seas of the world, p. 427–449. Elsevier Sci. Publ., Amsterdam.

Alvarez-Borrego, S., and R. Lara-Lara.
1991. The physical environment and primary productivity of the Gulf of California. *In* J. P. Dauphin and V. R. T. Simoneit (eds.), The Gulf and Peninsular province of the Californias: memoir 47, p. 555–567. Am. Assoc. Petroleum Geologists.

Aurioles, G. D., and A. Zavala G.
1994. Ecological factors that determine distribution and abundance of the California sea lion *Zalophus californianus*, in the Gulf of California. Ciencias Marinas 20:535–553.

Croxall, J. P., S. Rodwell, and I. L. Boyd.
1990. Entanglement in man-made debris of antartic fur seals at Bird Island, South Georgia. Mar. Mamm. Sci. 6:221–233.

Delgado-Estrella, A., J. G. Ortega-Ortiz, and A. Sánchez-Ríos.
1994. Varamientos de mamíferos marinos durante primavera y otoño y su relación con la actividad humana en el norte del Golfo de California. Anales del Instituto de Biología, Universidad Nacional Autónoma de México, serie Zoología 65:287–295.

Fowler, C. W.
1987. Marine debris and northern fur seals: a case study. Mar. Pollut. Bull. 18:326–335.

Hamman, M. G., J. S. Palleiro-Nayar, and O. Sosa-Nishizaki.
1995. The effects of the 1992 El Niño on the fisheries of Baja California, Mexico. Calif. Coop. Oceanic Fish. Invest. (CALCOFI) Report 36:127–133.

Harcourt, R. D. Aurioles, and J. Sánchez.
1994. Entanglement of California sea lions at Los Islotes, Baja California Sur, Mexico. Mar. Mamm. Sci. 101:122–125.

Heath, C. B., D. Aurioles, M. C. García, and A. Zavala.
1994. Factores que indican la disminución de la disponibilidad de presas de la población de lobos marinos en la Isla Ángel de la Guarda, México. Reunión Internacional para el estudio de los Mamíferos Marinos (Resúmenes) 19, 7 p.

LeBouf, B. J., D. Aurioles, R. Condit, C. Fox, R. Gisiner, R. Romero, and F. Sinsel.
1983. Size and distribution of the California sea lion population in Mexico. Proceedings of the California Academy of Sciences 43:77–85.

Morales V., B.
1990. Parámetros reproductivos del lobo marino en la Isla Angel de la Guarda, Golfo de California, México. M.Sc. thesis, Universidad Nacional Autónoma de México. México, D.F., 110 p.

Stewart, B. S., and P. K. Yochem.
1978. Entanglement of pinnipeds in synthetic debris and fishing net and line fragments at San Nicolas and San Miguel Islands, California. Mar. Pollut. Bull. 18:336–339.

Trites, A. W.
1992. Northern fur seals: why have they declined? Aquat. Mamm. 18:3–18.

Zar, J. H.
1974. Biostatistical analysis. Prentice Hall. Englewood Cliffs, NJ, 620 p.

Zavala, A. G.
1990. La población de lobo marino común, *Zalophus californianus* (Lesson 1828) en las islas del Golfo de California, México. B.Sc. thesis. Universidad Nacional Autónoma de México, México, D.F., 253 p.

Zavala G. A., A. Aguayo L., D. Aurioles G., and M. C. García R.
In press. Distribución y abundancia del lobo marino *Zalophus californianus californianus* (Lesson 1828), en el Golfo de California, México. Biótica.

Erratum

Quinn, T. P., J. L. Nielsen, C. Gan, M. J. Unwin, R. Wilmot, C. Guthrie, and F. M. Utter.
1996. Origin and genetic structure of chinook salmon, *Oncorhyncus tshawytscha*, transplanted from California to New Zealand: allozyme and mtDNA evidence. Fish. Bull. 94:506–521.

Corrections:

In Table 1 (p. 509) and Table 3 (p. 514):
Locus *PEP-B2**, Allele **108* should be
Locus *PEP-B1**, Allele **103*

In Table 4 (p. 516)
Locus *PEP-B2** should be
Locus *PEP-B1**

Superintendent of Documents Order Form

***5178**

☐ **YES,** please send me the following publications:

____ subscriptions to ***Fishery Bulletin (FB)***
for $32.00 per year ($40.00 foreign).

The total cost of my order is $_____. Price includes regular shipping and handling and is subject to change. International customers please add 25%.

Charge your order. It's easy!

Company or personal name (Please type or print)

Additional address/attention line

Street address

City, State, Zip code

Daytime phone including area code

Purchase order number (optional)

P3S

To fax your orders (202) 512–2250

Check method of payment:

❑ Check payable to Superintendent of Documents

❑ GPO Deposit Account ☐☐☐☐☐☐☐–☐

❑ VISA ❑ MasterCard

☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐

☐☐☐☐ (expiration date)

To phone your orders (202) 512–1800

Thank you for your order!

Authorizing signature

Mail To: Superintendent of Documents
P.O. Box 371954, Pittsburgh, PA 15250–7954

Fishery Bulletin

Guide for Contributors

Content

Articles published in *Fishery Bulletin* describe original research in fishery marine science, engineering and economics, and the environmental and ecological sciences, including modeling. Articles may range from relatively short to extensive; **notes** are reports of 5 to 10 pages without an abstract and describing methods or results not supported by a large body of data.

Although all contributions are subject to peer review, responsibility for the contents of papers rests upon the authors and not upon the editor or the publisher. It is therefore important that the contents of the manuscript are carefully considered by the authors.

Submission of an article is understood to imply that the article is original and is not being considered for publication elsewhere. Manuscripts should be written in English. Authors whose native language is not English are strongly advised to have their manuscripts checked by English-speaking colleagues prior to submission.

Preparation

Title page should include authors' full names and mailing addresses, the corresponding author's telephone, FAX number, and E-mail address, and a list of key words to describe the contents of the manuscript.

Abstract should not exceed one double-spaced typed page. It should state the main scope of the research but emphasize its conclusions and relevant findings. Because abstracts are circulated by abstracting agencies, it is important that they represent the research clearly and concisely.

Text must be typed double-spaced throughout. A brief introduction should portray the broad significance of the paper; the remainder of the paper should be divided into the following sections: **Materials and methods, Results, Discussion** (or **Conclusions**), and **Acknowledgments.** Headings within each section must be short, reflect a logical sequence, and follow the rules of multiple subdivision (i.e. there can be no subdivision without at least two items). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be spelled out the first time they are mentioned. The scientific names of species must be written out the first time they are mentioned; subsequent mention of scientific names may be abbreviated. Follow the *U.S. Government Printing Office Style Manual* (1984 ed.) and the *CBE Scientific Style and Format* (6th ed.) for editorial style, and the most current issue of the American Fisheries Society's *Common and Scientific Names of Fishes from the United States and Canada* for fish nomenclature. Dates should be written as follows: 11 November 1991. Measurements should be expressed in metric units, e.g., metric tons as (t); if other units of measurement are used, please make this fact explicit to the reader. The numeral one (1) should be typed as a one, not as a lower-case el (l). Use of appendices is discouraged.

Text footnotes should be numbered with Arabic numerals. Footnote all personal communications, unpublished data, and unpublished manuscripts with full address of the communicator or author, or, as in the case of unpublished data, where the data are on file. Authors are advised to avoid references to nonstandard (gray) literature, such as internal, project, processed, or administrative reports. Where these references are used, please include whether they are available from NTIS (National Technical Information Service) or from some other public depository.

Literature cited comprises published works and those accepted for publication in peer-reviewed literature (in press). Follow the name and year system for citation format. In the text, cite as follows: Smith and Jones (1977) or (Smith and Jones, 1977). If there is a sequence of citations, list by year: Smith, 1932; Smith and Jones, 1985; Smith and Allen, 1986. Abbreviations of serials should conform to abbreviations given in *Serial Sources for the BIOSIS Previews Database.* Authors are responsible for the accuracy and completeness of all citations.

Tables should not be excessive in size and must be cited in numerical order in the text. Headings should be short but ample enough to allow the table to be intelligible on its own. All unusual symbols must be explained in the table legend. Other incidental comments may be footnoted with italic numerals. Use the asterisk only to indicate probability in statistical data. Because tables are typeset, they need only be submitted typed and formatted, with double-spaced legends. Zeros should precede all decimal points for values less than one.

Figures must be cited in numerical order in the text. The senior author's last name and the figure number should be written on the back of each one. Illustrations should be submitted as originals and not as photocopies. Submit photographs as glossy prints or slides that show good contrast, otherwise we cannot guarantee a good final printed copy. We may need to edit electronically generated graphics; therefore do not submit them as encapsulated postscript (EPS) files. Save them in the software program in which they were created. Label all figures with Helvetica typeface and capitalize the first letter of the first word in axis labels. Italicize species name and variables in equations. Use zeros before all decimal points. Use Times Roman bold typeface to label the parts of a figure. Send only photocopies of figures to the Scientific Editor; original figures will be requested when the manuscript has been accepted for publication. Each figure legend should explain all symbols and abbreviations in the figure and should be double-spaced and placed at the end of the manuscript.

Copyright law does not cover government publications; they fall within the public domain. If an author reproduces any part of a government publication in his work, reference to source is appreciated.

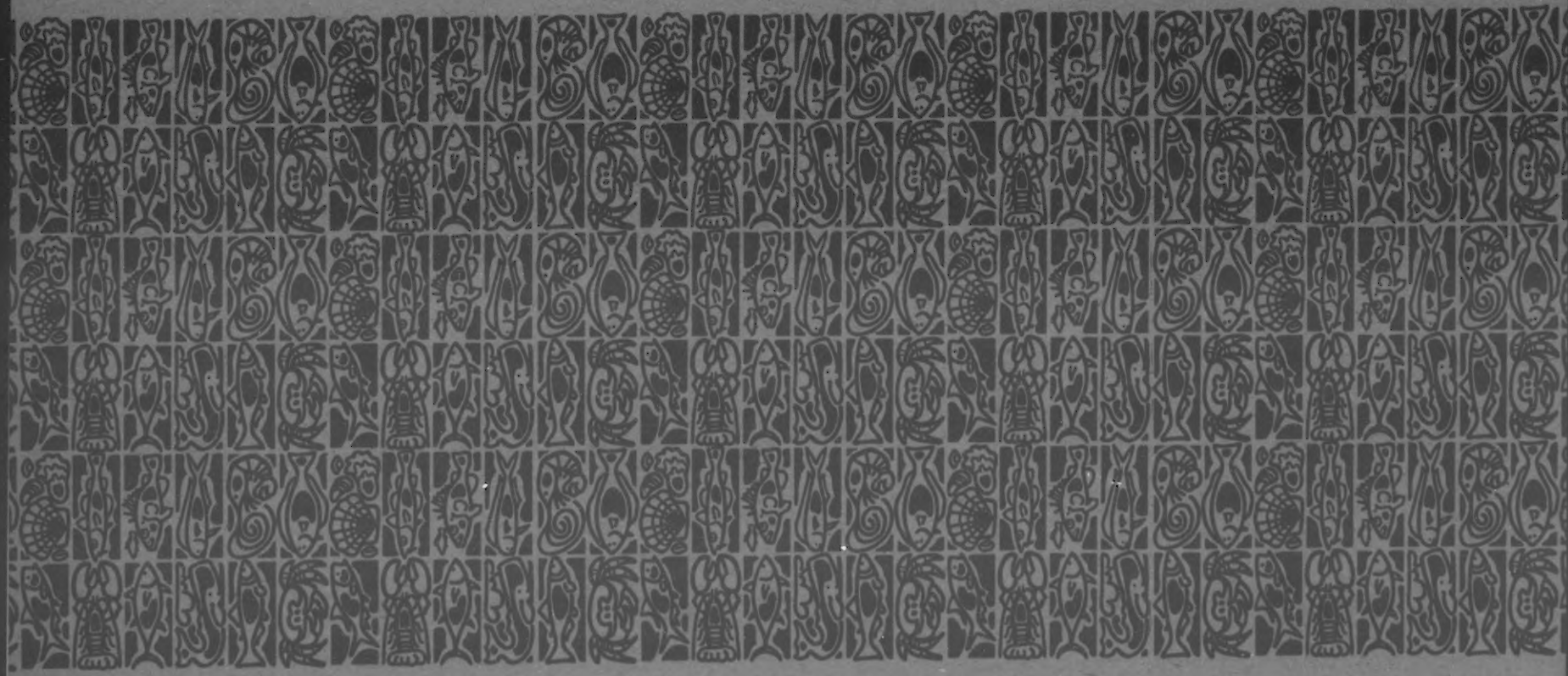
Submission

Send printed copies (original and three copies) to the Scientific Editor:

Dr. John B. Pearce, Scientific Editor
Northeast Fisheries Science Center
National Marine Fisheries Service
166 Water Street
Woods Hole, MA 02543-1097

Once the manuscript has been accepted for publication, you will be asked to submit a software copy of your manuscript to the Managing Editor. The software copy should be submitted in *WordPerfect* or *Microsoft Word* text format (or in standard ASCII text format if neither program is available) and placed on a 5.25-inch or 3.5-inch disk that is double-sided, double or high density, and that is compatible with either DOS or Apple Macintosh systems.

A copy of page proofs will be sent to the author for final approval prior to publication.

Copies of published articles and notes are available free of charge to the senior author (50 copies) and to his or her laboratory (50 copies). Additional copies may be purchased in lots of 100 when the author receives page proofs.

☆ U.S. Gov. Printing Office 1996
790-016/40004